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An exploration of *Echinoderes* (Kinorhyncha: Cyclorhagida) in Korean and neighboring waters, with the description of four new species and a redescription of *E. tchefouensis* Lou, 1934*

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Abstract

A large collection of kinorhynch specimens from coastal and subtidal localities around the Korean Peninsula and in the East China Sea was examined, and the material included several species of undescribed or poorly known species of *Echinoderes* Claparède, 1863. The present paper is part of a series dealing with echinoderid species from this material, and includes descriptions of four new species of *Echinoderes*, *E. aspinosus* **sp. nov.**, *E. cernunnos* **sp. nov.**, *E. microaperturus* **sp. nov.** and *E. obtuspinosus* **sp. nov.**, and redescription of the poorly known *Echinoderes tchefouensis* Lou, 1934.

Key words: East Sea, East China Sea, kinorhynch, Korea, meiofauna, taxonomy

Introduction

Echinoderes Claparède, 1863 appears to be the most diverse genus within the Kinorhyncha. Species of this genus have been found in most marine benthic substrates, on latitudes ranging from the Arctic to the tropics, and from the intertidal zone down to the deep sea. Still, our information about their global distribution is extremely fragmented, as is our knowledge about their total biodiversity. As it is the case with most other minor meiofaunal taxa, our current knowledge about their geographical distribution is to a great extent a reflection of the activities of the few experts that have addressed the group through time. For the genus *Echinoderes* and its closest relatives, we can consider the east American coast, from Maine to Belize, relatively well-examined thanks to a lifelong effort of Robert P. Higgins (see, e.g., Higgins 1964, 1977, 1983). Also the Mediterranean and West European coasts are relatively well-explored through the pioneering work of Zelinka (1928), as well as more recent efforts of Higgins (1978, 1985), Huys & Coomans (1989), Pardos *et al.* (1998), GªOrdóñez *et al.* (2008), and Herranz *et al.* (2012).

The best explored region in East Asia is probably the area between Southeast Russia, the Korean Peninsula and Japan. *Echinoderes* around Korea, and in neighboring Russian and Japanese waters, have first of all been addressed in several studies facilitated by A. V. Adrianov. He has described two species from Korean waters, *E. koreanus* Adrianov, 1999 in Adrianov & Malakhov (1999) and *E. ulsanensis* Adrianov, 1999 in Adrianov & Malakhov (1999), and additional four from nearby Japanese or Russian localities that very well could occur around the Korean Peninsula as well: *Echinoderes multisetosus* Adrianov, 1989, *E. filispinosus* Adrianov, 1989, *E. aureus* Adrianov, Murakami & Shirayama, 2002a, *E. sensibilis* Adrianov, Murakami & Shirayama, 2002b. Besides the contributions of Adrianov and collaborators, other studies have also added to our knowledge about kinorhynch biodiversity in the region. *Echinoderes tchefouensis* Lou, 1934 was described from nearby Chinese waters (see also

Higgins & Kristensen 1988). More recently *E. lanceolatus* Chang & Song, 2002 was described and reported from numerous localities in Korea, and most recently *E. rex* Lundbye, Rho & Sørensen, 2011 was described from a locality in the Korea Strait. Hence, with nine known species, the fauna of *Echinoderes* in Korea and nearby waters could perhaps be considered relatively well-known—at least compared to our knowledge about most other regions.

However, ongoing studies show that the Korean kinorhynch fauna is far from being well-described. Various non-echinoderid new species from Korea have recently been described in a series of papers (Sørensen *et al.* 2010a, 2010b, 2010c), and the next step in this survey has now been reached, with an attempt to approach the diverse composition of *Echinoderes* in these samples. Kinorhynchs from more than 70 samples taken in Korean or nearby waters have been examined, and the present paper represents the first contribution about *Echinoderes* new to Korea. It includes the description of four species new to science, and a redescription of *E. tchefouensis* that previously has been known from its Chinese type locality only. Descriptions of additional new species of *Echinoderes* and closely related genera are currently being carried out, which indicates that the Korean waters still have much kinorhynch biodiversity to reveal.

Materials and methods

During the ongoing exploration of the Asian kinorhynch fauna, specimens from more than 70 localities have been examined. Twenty-two of these yielded specimens for the present study (Table 1). A vast majority of the stations are concentrated within Korean territories, representing a dense sampling along the Korean east coast, numerous samples from the Korea Strait and around Jeju Island south of the Peninsula, along the Korean south coast, and to a lesser extend along the west coast. Several samples furthermore originate from the East China Sea, whereas a few sporadic samples were taken even further away, including a few from Saipan, Micronesia, the Philippines and the Malaysian part of Borneo. Since parts of this study is still being carried out, and kinorhynchs from several localities remain to be described in future contributions, the overview of stations provided here, see Fig. 1 and Table 1, only includes the 22 stations that are relevant for the present study.

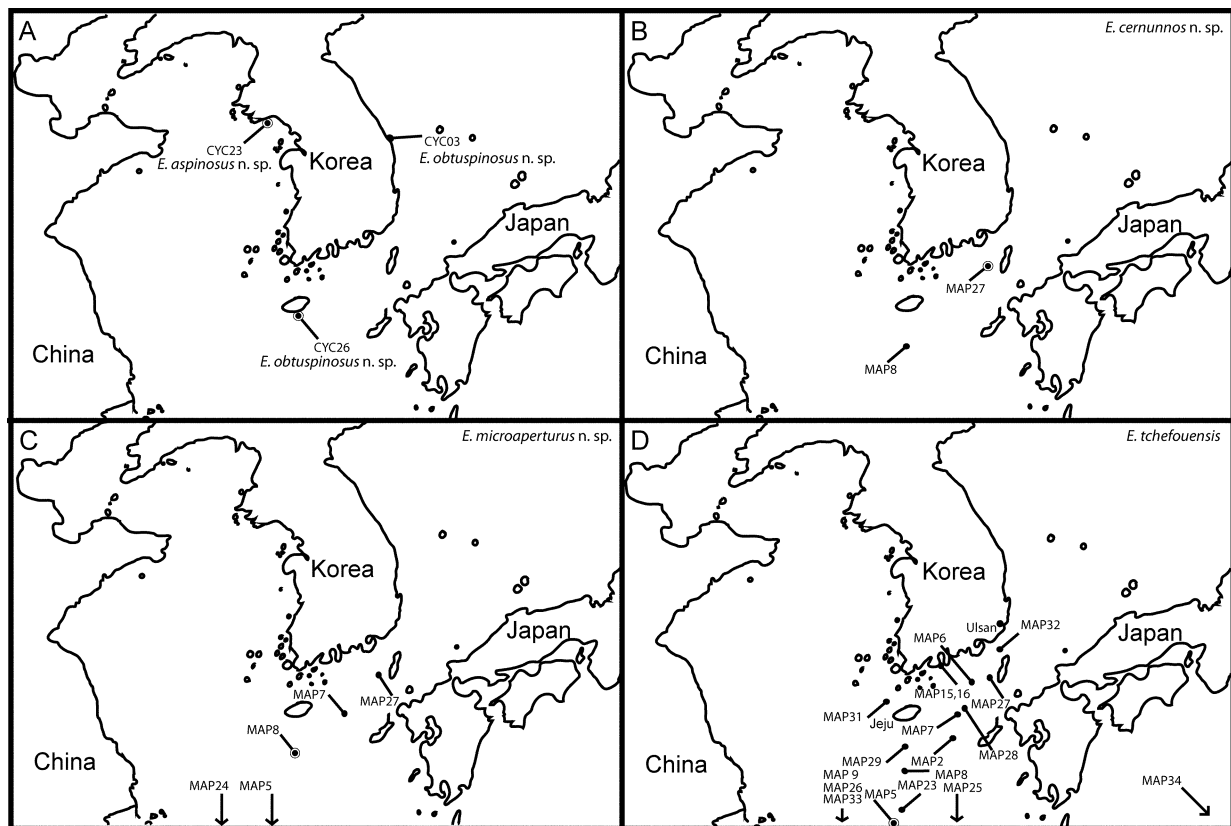


FIGURE 1. Maps showing collecting localities for: A, *Echinoderes aspinosus* **sp. nov.** and *Echinoderes obtuspinosus* **sp. nov.**; B, *Echinoderes cernunnos* **sp. nov.**; C, *Echinoderes microaperturus* **sp. nov.**; D, *Echinoderes tchefouensis* Lou, 1934. Type localities are marked with a ring around the dot.

TABLE 1. Summary of data on collecting localities, methods, specimen processing and deposition. Species with boldfaced names were recorded in the present study. *) after a species name indicates that holotype/neotype originates from this locality. Other superscript numbers refer to previous reports of species from the same localities: ¹⁾ Sørensen *et al.* (2010a), ²⁾ Sørensen *et al.* (2010b), ³⁾ Sørensen *et al.* (2010c), ⁴⁾ Sørensen *et al.* (2012).

Station name	Location	Date	Position	Depth	Sediment type	Collecting gear	Sample processing	Fixation	Kinorhynchs recorded	Collector	Deposition of specimens
CYC-03	Harbor in Geumjin, 18 km SE of Gangneung, East Sea, Korea	Nov 5 1999	37°39.13'N 129°03.00'E	–	Rinsed off hermit crab	Smith-MacIntyre grab	–	5% formalin	<i>Echinoderes obtuspinosus</i>	Chang, Lee & Song	NHMD, Acc. No.: ZMUC KIN 549-550
CYC-23	Yeonpyeong Isl., W of Seoul and Incheon, West Sea, Korea	Mar 31 2001	37°39.05'N 125°41.43'E	–	Subtidal sands	Smith-MacIntyre grab	MgCl anaesthetization and freshwater shocking	5% formalin	<i>Echinoderes aspinosus</i> *)	Park	NIBR, Acc. No.: INBRIV0000245081 NHMD, Acc. No.: ZMUC KIN 538
CYC-26	Munseum Islet, Jeju Island, Korea Strait	Feb 26 1999	33°13.52'N 126°33.92'E	–	Rinsed off algae	Smith-MacIntyre grab	–	5% formalin	<i>Echinoderes obtuspinosus</i> *)	Lee & Song	NIBR, Acc. No.: INBRIV0000245084
MAP-02	Korea Strait	Sep 10 2006	32°49.42'N 127°43.27'E	140 m	Mud	Box corer	Ludox centrifugation	4% formalin	<i>Echinoderes tchefouensis</i>	HSR	MVS pers. coll.
MAP-05	East China Sea	Sep 28 2006	30°31.66'N 125°55.86'E	79 m	Mud	Box corer	Ludox centrifugation	4% formalin	<i>Condyloderes cf. setoensis</i> , <i>E. microaperturus</i> , <i>E. tchefouensis</i> *)	HSR	NHMD, Acc. No.: ZMUC KIN 468-472, KIN547-548. MVS and CYC personal collection
MAP-06	East China Sea	Sep 6 2006	34°10.24'N 128°25.90'E	79 m	Mud	Box corer	Ludox centrifugation	4% formalin	<i>Condyloderes megastigma</i> ³⁾), <i>Echinoderes tchefouensis</i>	HSR	NHMD, Acc. No.: ZMUC KIN150, KIN 473-474. MVS pers. coll.
MAP-07	Korea Strait	Sep 30 2006	33°18.91'N 127°40.96'E	132 m	Mud	Box corer	Ludox centrifugation	4% formalin	<i>Condyloderes cf. paradoxus</i> , <i>Echinoderes microaperturus</i> , <i>E. tchefouensis</i>	HSR	NHMD, Acc. No.: ZMUC KIN 480. MVS pers. coll.
MAP-08	Korea Strait	Jun 6 2008	32°21.59'N 126°46.32'E	113 m	Mud	Box corer	Ludox centrifugation	4% formalin	<i>Echinoderes cernuus</i> , <i>E. microaperturus</i> *), <i>E. tchefouensis</i>	HSR	NHMD, Acc. No.: ZMUC KIN 475-479; 536-537; KIN 40-544; NIBR, Acc. No.: INBRIV0000245083. MVS personal collection
MAP-09	Sipadan, Borneo, Malaysia	Apr 25 2002	04°07.04'N 118°37.38'E	13 m	Coral Sands	Scuba	Stewing	4% formalin	<i>Echinoderes tchefouensis</i>	HSR	MVS pers. coll.
MAP-15	South of Gamak Bay, Korean south coast	May 26, 2008	34°34.43'N 127°45.52'E	13 m	Mud with shells	Smith-MacIntyre grab	Ludox + centrifugation	4% formalin	<i>Dracoderes abei</i> ⁴⁾ , <i>E. tchefouensis</i> , <i>Kinorhynchus</i> sp. ⁴⁾ , <i>Pycnophyes</i> sp. ⁴⁾	HSR+WM	NHMD, Acc. No.: ZMUC KIN 502-508, KIN 545. MVS & HSR personal collection
MAP-16	Geum-do, Korean south coast	May 26, 2008	34°32.05'N 127°45.88'E	9 m	Mud	Smith-MacIntyre grab	Ludox + centrifugation	4% formalin	<i>Echinoderes tchefouensis</i>	HSR+WM	MVS personal collection
MAP-23	East China Sea	Aug 6, 2008	31°22.61'N 126°03.03'E	73 m	Mud	Box corer	Ludox + centrifugation	4% formalin	<i>Echinoderes tchefouensis</i>	HSR	NHMD, Acc. No.: ZMUC KIN 481-486. MVS personal collection

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TABLE 1. (Continued)

Station name	Location	Date	Position	Depth	Sediment type	Collecting gear	Sample processing	Fixation	<i>Kinorhynchs recorded</i>	Collector	Deposition of specimens
MAP-24	East China Sea	Aug 6, 2008	30°19.86'N 125°17.06'E	74 m	Mud	Box corer	Ludox + centrifugation	4% formalin	<i>Echinoderes microaperturus</i>	HSR	NHMD, Acc. No.: ZMUC KIN 539-545, 546. HSR and CYC personal collection
MAP-25	East China Sea	Aug 6, 2008	28°32.69'N 125°09.53'E	104 m	Mud	Box corer	Ludox + centrifugation	4% formalin	<i>Dracoderes abei</i> ⁴⁾ , <i>Condyloderes</i> sp. ⁴⁾ , <i>Echinoderes tchefouensis</i> , <i>Pycnophyes</i> sp. ⁴⁾	HSR	NHMD, Acc. No.: ZMUC KIN 555-558. MVS personal collection
MAP-26	East China Sea	Aug 8, 2008	32°06.93'N 125°11.19'E	57 m	Mud	Box corer	Ludox + centrifugation	4% formalin	<i>Echinoderes tchefouensis</i> , <i>Dracoderes abei</i>	HSR	NHMD, Acc. No.: ZMUC KIN 551-553. CYC & HSR personal collection
MAP-27	Korea Strait	Oct 6, 2008	34°16.41'N 128°40.40'E	96 m	Mud with tiny shells	Box corer	Ludox centrifugation	4% formalin	<i>Echinoderes cernunnos</i> ^{*)} , <i>E. microaperturus</i> , <i>E. tchefouensis</i>	HSR	NIBR, Acc. No.: INBRIV000245082; NHMD, Acc. No.: ZMUC KIN 560-564. MVS personal collection
MAP-28	Korea Strait	Oct 6, 2008	33°44.51'N 128°15.39'E	126 m	Mud with tiny shells	Box corer	Ludox centrifugation	4% formalin	<i>Echinoderes tchefouensis</i> , <i>Pycnophyes</i> sp.	HSR	MVS personal collection
MAP-29	Korea Strait	Oct 6, 2008	32°37.49'N 126°42.24'E	118 m	Mud with tiny shells	Box corer	Ludox centrifugation	4% formalin	<i>Echinoderes tchefouensis</i> , <i>Pycnophyes</i> sp.	HSR	NHMD, Acc. No.: ZMUC KIN 565-566. MVS personal collection
MAP-31	Korea Strait	Oct 8, 2008	33°40.33'N 126°04.33'E	103 m	Mud	Box corer	Ludox centrifugation	4% formalin	<i>Condyloderes megastigma</i> ³⁾ , <i>Echinoderes tchefouensis</i> , <i>Paracentrophyes anurus</i> ¹⁾ , <i>Pycnophyes</i> sp. ³⁾ , <i>Sphenoderes poseidon</i> ³⁾ .	HSR	NHMD, Acc. No.: ZMUC KIN 251, KIN 341-343. MVS personal collection
MAP-32	Korea Strait	Oct 6, 2008	34°47.19'N 129°05.58'E	109 m	Mud with tiny shells	Box corer	Ludox centrifugation	4% formalin	<i>Condyloderes megastigma</i> ³⁾ , <i>Echinoderes tchefouensis</i> , <i>Pycnophyes</i> sp.	HSR	MVS personal collection
MAP-33	Batangas, Philippines	Feb 6, 2006	13°36.53'N 120°56.52'E	62 m	Coral sand	Box corer	Ludox centrifugation	4% formalin	<i>Echinoderes tchefouensis</i>	HSR	MVS personal collection
MAP-34	Managaha Island, Saipan	Jun 3, 1996	15°14.47'N 145°42.63'E	0 m	Coral sand	By hand	Freshwater shocking	4% formalin	<i>Echinoderes tchefouensis</i> , <i>Tridionoderes anulap</i>	HSR	MVS personal collection

Table 1 presents all relevant data, regarding locality information, sampling methods and processing, collected species and deposition of specimens. Sample numbers with the prefix 'CYC' all originate from the collections of author C. Y. Chang, whereas stations with the name 'MAP' originate from author H. S. Rho. This station terminology has not been used in previous contributions, but to ease cross referencing between stations in future publications, we will from now on attempt to follow this station terminology.

Specimens were collected and processed as specified in Table 1. For preparation of light microscopical (LM) slides, specimens collected by CYC were generally dehydrated in a solution of 5% glycerin and 95% ethyl alcohol, and subsequently mounted in glycerine on an H-S slide. Specimens collected by HSR were dehydrated through a graded glycerin series and mounted in Fluoromount G on a glass slides. Specimens for LM were examined and photographed using Nomarski differential interference contrast with an Olympus BX51 microscope, equipped with an Olympus DP20 camera and a drawing tube. Measurements were made with Cell[^]D software.

Specimens for scanning electron microscopy (SEM) were dehydrated through a series of alcohol, and subsequently transferred to acetone through a graded alcohol/acetone series. When contained in 100% acetone, the specimens were critical point dried, mounted on aluminium stubs, sputter coated with gold or a platinum/palladium mix and examined with a JEOL JSM-6335F Field Emission scanning electron microscope.

The terminology in the taxonomic account generally follows Neuhaus & Higgins (2002), Sørensen & Pardos (2008), and the most recent papers of the first author. The term IJ-line refers to the transverse position on a segment that denotes the intersegmentary joint between this and the following segment (Thormar & Sørensen 2010; Herranz *et al.* 2012). Glandular cell outlet type 1, pore field, or simply gco1 refers to a structure that in LM appears like one (or sometimes several) small rounded marking in the cuticle (e.g. Figs 9C, 14F), whereas in SEM it looks like a small, porous, slightly depressed area. Glandular cell outlets type 2, or gco2, appear much more conspicuous in both LM and SEM. In LM they look like more distinct markings, and they often tend to be wedge-shaped (e.g. Fig. 14A) or form a transverse line (e.g. Fig. 5A), whereas they in SEM appear as large openings, often with a reinforced anterior margin (e.g. Figs 10D, 14D–F). The terms were introduced by Neuhaus & Blasche (2006), but the structures have also been mentioned occasionally and less systematically in previous contributions, e.g., as “muscular scars” or “cuticular scars” (see, e.g., Higgins 1985). The “type 2 gland pore” described by G^oOrdóñez *et al.* (2000) may also represent a slightly modified version of the gco2. The structures have not previously been subject of much interest, but as indicated in the following descriptions, especially glandular cell outlet type 2 may have great taxonomic significance, and they probably represent characters with same taxonomic importance as spines and tubules.

All examined material is deposited at the National Institute of Biological Resources, Korea (NIBR), at the Natural History Museum of Denmark (NHMD), or stored in the personal collections of one of the authors, HSR, CYC or MVS.

Taxonomic account

Order Cyclorhagida Zelinka, 1896

Family Echinoderidae Bütschli, 1876

Genus *Echinoderes* Claparède, 1863

Echinoderes aspinosus sp. nov.

(Figures 2–3, Table 2)

Diagnosis. *Echinoderes* without tubules or spines, except lateral terminal ones. Both sexes with rather thin lateral terminal spines; females furthermore with extremely thin lateral terminal accessory spines. Pectinate fringe on ventral side of segments 2 to 5 very strong and obliquely orientated, pointing towards the midventral line. Sieve plates on segment 9 elongate and narrow, reaching almost 50% of the total segment length.

Type material. Holotype: adult female, collected on 31 March 2001, at station CYC-23, Yeonpyeong Island off the Korean west coast, (Fig. 1A), 37°39.05'N 125°41.43'E, Korea, from subtidal sand, mounted in glycerine, deposited at NIBR under accession number INBRIV0000245081. Allotype: adult male, same collecting data as holotype, mounted in glycerine, deposited at NHMD under accession number ZMUC KIN-538. No specimens were available for examination with SEM.

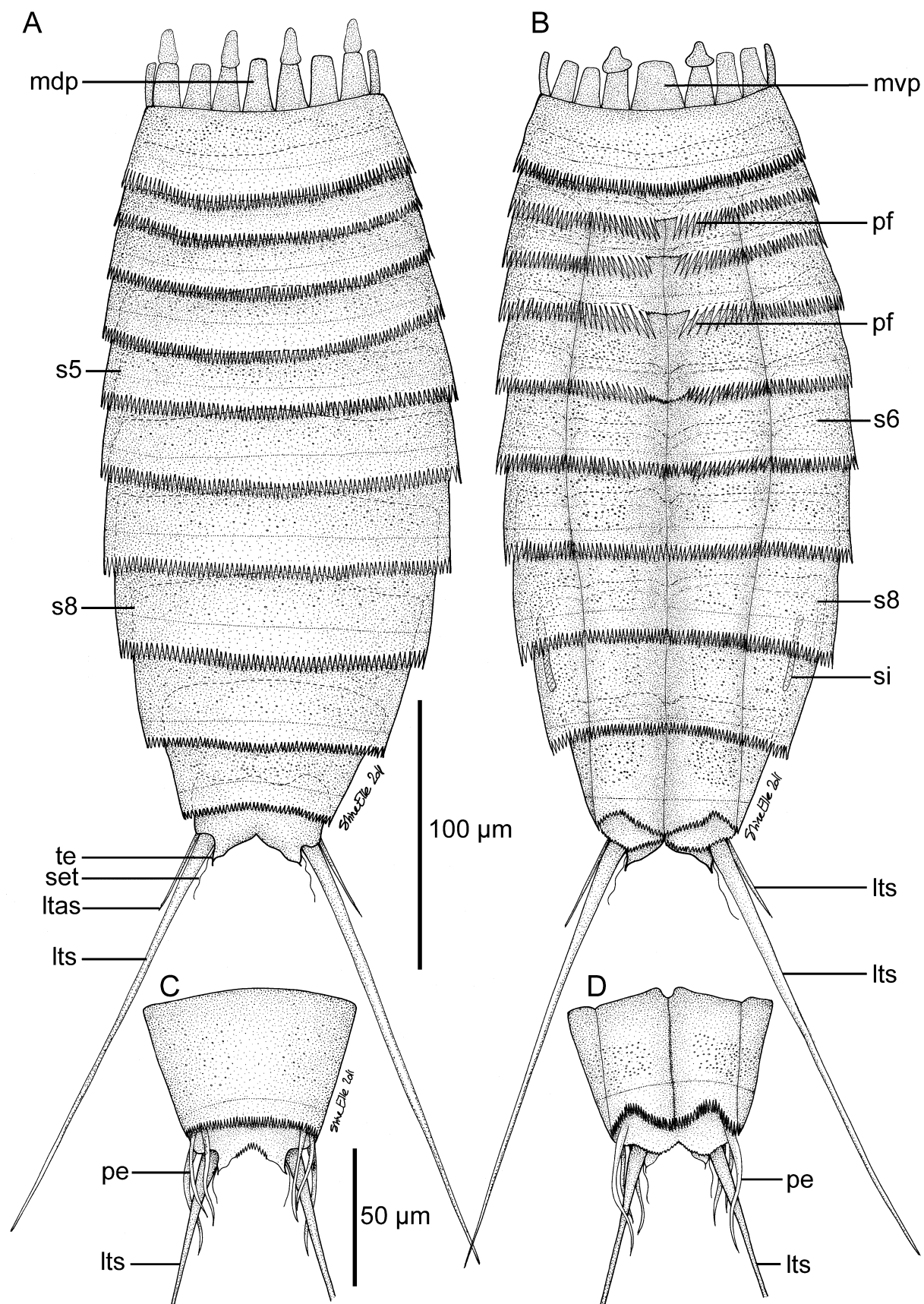


FIGURE 2. Line art illustrations showing general habitus in *Echinoderes aspinosus* sp. nov.: A, female, dorsal view; B, female, ventral view; C, segments 10 and 11 in male, dorsal view; D, segments 10 and 11 in male, ventral view. Abbreviations: ltas, lateral terminal accessory spine; lts, lateral terminal spine; mdp, middorsal placid; mvp, midventral placid; pe, penile spines; pf, pectinate fringe; s, segment followed by segment number; set, seta; si, sieve plate; te, tergal extension.

Etymology. The species name is composed of the Latin *a-* (no or lacking) and *-spina* (spine), meaning the one without spines, with reference to the complete absence of spines on segments 1 to 10.

Description. Adult specimens consist of a head, a neck and eleven trunk segments (Figs 2A–B, 3D). Measurements and dimensions are given in Table 2. A table summarizing sensory spots, spines, and glandular cell outlet positions is not provided, since such structures apparently are absent (or could at least not be identified) on most of the animal. Because no specimens were available for SEM examinations, it was not possible to identify minor cuticular structures such as sensory spots and pore fields. Hence, not mentioning these structures in the description should not be understood as a positive confirmation of their absence.

TABLE 2. Measurements of female holotype and male allotype of *Echinoderes aspinosus* **sp. nov.** from Yeonpyeong Island (CYC-23). Abbreviations: LTS: lateral terminal spine; MSW-7: Maximum sternal width, measured on segment 7 in this species; S: segment lengths; SW-10, standard width, always measured on segment 10; TL: trunk length.

Character	Length Holotype	Length Allotype
TL	284 μm	263 μm
MSW-7	72 μm	66 μm
MSW-7/TL	25.4 %	25.1 %
SW-10	57 μm	50 μm
SW-10/TL	20.1 %	19.0 %
S1	30 μm	29 μm
S2	32 μm	30 μm
S3	37 μm	33 μm
S4	42 μm	37 μm
S5	45 μm	41 μm
S6	51 μm	47 μm
S7	55 μm	52 μm
S8	61 μm	59 μm
S9	60 μm	58 μm
S10	47 μm	47 μm
S11	33 μm	28 μm
LTS	156 μm	146 μm
LTS/TL	54.9 %	55.5 %

The head consists of a retractable mouth cone and an introvert. Inner and outer armature could not be examined in detail. The pharynx of the holotype was strongly protruded though, revealing the presence of a pharyngeal crown (Fig. 3A).

The neck consists of 16 placids, all measuring 18 μm in length and 10 μm in width at bases (Figs 2A, 3B), except midventral placid that measures 16 μm in width (Figs 2B, 3C). If the midventral placid is number 1, and other placids are numbered clockwise from this one, placids number 2 and 16 have broad trichoscalid plates, whereas smaller, but rather elongate trichoscalid plates are associated with placids number 6, 8, 10 and 12 (Figs 2A, 3B).

Segment 1 consists of one complete cuticular ring (Figs 2A–B, 3B–C). Sensory spots or pore fields could not be identified with certainty. Cuticular hairs emerge through rounded perforation sites, and are densely scattered over the posterior half of the segment, down to the IJ-line. Posterior margin with well-developed pectinate fringe.

Segment 2 consists of one complete cuticular ring. Cuticular hairs are distributed in a median belt around the segment, limited posteriorly by the IJ-line. Posterior segment margin with regular pectinate fringe on dorsal side, but a conspicuously strong fringe ventrally; fringe tips within the ventromedial areas are obliquely orientated, pointing towards the midventral line (Figs 2C, 3C).

Segment 3, and following 8 segments, consist of one tergal and two sternal plates (Figs 2B, 3B). Spines, tubules, glandular cell outlets type 1 or 2 are not present. Cuticular hairs are densely distributed in a median belt around the segment, except in paraventral areas, limited posteriorly by the IJ-line. Posterior margin with regular pectinate fringe on dorsal side, and a conspicuously strong one on ventral side; fringe tips on sternal plates of segments 3 to 5 are obliquely orientated, pointing towards the midventral line (Figs 2B, 3E); fringe tips on sternal plates of following segment not oblique and less prominent (Figs 2B, 3F).

Segment 9 similar to preceding segments, but with weaker pectinate fringe, and a pair of very conspicuous sieve plates (Figs 2B, 3F). The sieve plates are elongate, 27 μm long, i.e. almost 50% of segment length, and rather narrow, but broadens slightly in each end.

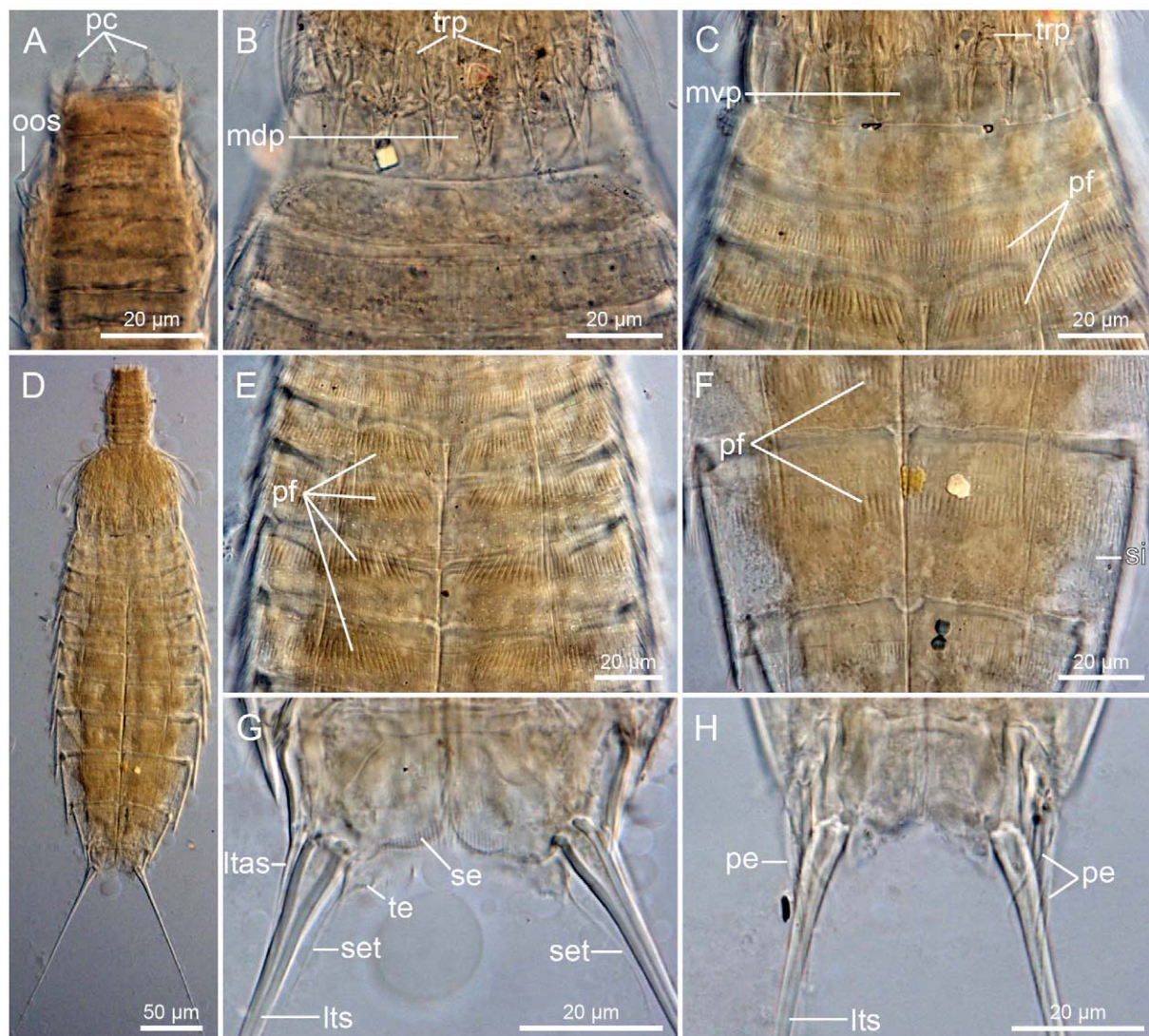


FIGURE 3. Light micrographs showing details in neck and trunk morphology of *Echinoderes aspinosus* **sp. nov.**, displaying female holotype, NIBR Acc. No. INBRIV0000245081 (A, C–G) and male allotype, ZMUC KIN-538 (B, H): A, detail of extended mouth cone; B, neck and segments 1 and 2, dorsal view; C, neck and segments 1 and 2, ventral view; D, ventral overview of holotype; E, Segments 2 to 5, ventral view; F, Segments 8 and 9, ventral view; G, Segment 11 and terminal spines in female; H, Segment 11 and terminal spines in male. Abbreviations: ltas, lateral terminal accessory spine; lts, lateral terminal spine; mdp, middorsal placid; mvp, midventral placid; oos, outer oral style; pc, pharyngeal crown; pe, penile spine; pf, pectinate fringe; se, sternal extension; set, seta; te, tergal extension; trp, trichoscalid plate.

Segment 10 generally as preceding segments, but with the posterior margins of the sternal plates forming a broadly lobed midventral extension that almost covers the ventral side of the terminal segment (Fig. 2B).

Segment 11 with long and rather thin lateral terminal spines. Females furthermore with pair of very thin lateral terminal accessory spines (Figs 2A–B, 3G). Males with three pairs of flexible penile spines; dorsalmost spine thick, ca. 30 µm long, median penile spine slightly thinner and pointed, ca. 26 µm, ventralmost penile spine thicker, ca. 41 µm (Figs 2C–D, 3H). Cuticular hairs are not present. Tergal extensions are short, with interrupted mesial margins (Fig. 3G); sternal extensions short and lobed with weak fringes. A pair of long (23 µm) setae emerges from the outer margins of the tergal extensions (Figs 2A, 3G).

Notes on diagnostic features and potential relatives. Due to its complete lack of tubules and spines (except terminal ones), *Echinoderes aspinosus* **sp. nov.** cannot be confused with any other species of Echinoderidae. In addition to this negative character, the species can also be recognized by its strong, obliquely orientated pectinate fringe on the ventral side of segments 2 to 5. This character has to our knowledge not been reported from any other kinorhynch species. Another noteworthy character, not unique though, is the enlarged sieve plates.

The only species that potentially could be confused with *E. aspinosus* **sp. nov.**, are those of the *E. coulli*-group that also tend to have few, small or completely reduced spines and tubules (Ostmann *et al.* 2012). This species-group includes, besides *E. coulli* Higgins, 1977, the following five species: *E. maxwelli* Omer-Cooper, 1957, *E. teretis* Brown, 1999 in Adrianov & Malakhov, 1999, *E. rex*, *E. applicitus* Ostmann, Nordhaus & Sørensen, 2012, and *E. ohtsukai* Yamasaki & Kajihara, 2012. Common for all these six species are, besides the reduced spines in terms of number and size, that they all possess a somewhat enlarged sieve plate, and that females do not possess lateral terminal accessory spines (see Higgins 1977; Lundbye *et al.* 2011, Ostmann *et al.* 2012, Yamasaki & Kajihara 2012). An enlarged sieve plate is found in *E. aspinosus* **sp. nov.** also, and even though females of the species have lateral terminal accessory spines, it is noteworthy that they are very weakly developed. These similarities could indicate a closer relationship between *E. aspinosus* **sp. nov.** and species of the *E. coulli*-group.

***Echinoderes cernunnos* sp. nov.**

(Figures 4–6, Tables 3–4)

Diagnosis. Segments 1 and 2 consisting of closed rings; segments 3 to 10 of one tergal and two sternal plates, and segment 11 consisting of two tergal and two sternal plates. Specimens with middorsal spines on segment 4–8, gradually increasing in length towards the more posterior segments; lateroventral tubule on segment 5; lateroventral spines on segments 6–9; very short, laterodorsal, distally fringed elements (tubules?) on segment 10. Glandular cell outlets type 2 present in subdorsal, laterodorsal, sublateral and ventrolateral positions on segment 2, midlateral positions on segments 5 and 7, and in sublateral position of segment 8. Tergal extension of segment 11 extremely elongated, forming strong, horn-like extensions.

Type material. Holotype: adult female, collected on 6 October 2008, at station MAP-27, in the Korea Strait between Tsushima Island and the Korean mainland (Fig. 1B), 34°16.41'N 128°40.40'E, from mud with tiny shells at 96 m depth, mounted in Fluoromount G, deposited at NIBR under accession number INBRIV0000245082. No allotype designated. Paratypes: two females, collected on 6 June 2008 from station MAP-08 in the East China Sea, ca. 100 km south of Jeju Island, (Fig. 1B), 32°21.59'N 126°46.32'E, from mud at 113 m depth, mounted in Fluoromount G (one in lateral position), deposited at NHMD under accession number ZMUC KIN-536 and KIN-537.

Additional material. One female from the same locality as the holotype, mounted for SEM and stored in the personal collection of MVS.

Etymology. The species is named after Cernunnos—The Horned God—from Celtic mythology, inspired by the species' diagnostic long, horn-like tergal extensions.

Description. Adult specimens consist of a head, a neck and eleven trunk segments (Figs 4A–B, 6A). Trunk cuticle appears relatively thin and flexible. Measurements and dimensions are given in Table 3. A summary of sensory spot, spine, tubule and glandular cell outlet positions is provided in Table 4.

The head consists of a retractable mouth cone and an introvert. Inner oral styles are clearly present, but their exact arrangement could not be examined. Outer armature with nine outer oral styles composed of two subunits. Bases of outer oral styles with a single fringe, flanked by a pair of off-set spikes (Fig. 6B). The arrangement of scalids on the introvert (Fig. 6C) is identical with the one found in *E. microaperturus* **sp. nov.** (see Fig. 8 and description below) and several other species described herein. Leaf-like scalids (see definition under description of the following species) are present as single ones in sections 1, 5, 6 and 7, and pairs in sections 3 and 9. A distinct band of longitudinal ridges that extend into fringe tips stretches around the introvert at the level between Rings 05 and 06 (Fig. 6C).

The neck consists of 16 placids, all measuring 12 µm in length and 7 µm in width at bases (Figs 4A–B, 5A–B), except midventral placid that measures 11 µm in width (Figs 4B, 5B). Placids number 2 and 16 (counting clockwise from midventral placid) with broad trichoscalid plate and attached trichoscalid (Fig. 5B). Smaller trichoscalid plates with trichoscalids on placids number 6, 8, 10, and 12 (Figs 4A, 5A).

Segment 1 consists of one complete cuticular ring (Figs 4A–B, 5A–B). Pairs of subdorsal (Fig. 5A), laterodorsal (Fig. 6D) and ventromedial (Fig. 4B) sensory spots present. Sensory spots are small and rounded, with numerous papillae. Only few cuticular hairs present; hairs emerge through rounded perforation sites, and are scattered around the segment (Fig. 6D). Posterior margin with pectinate fringe; fringe appears serrated on its dorsal side, whereas the ventral fringe tips extend into filiform tips.

TABLE 3. Measurements of female holotype and two female paratypes of *Echinoderes cernunnos* **sp. nov.** from the Korea Strait (MAP-27) and East China Sea (MAP-08). Abbreviations: (ac): acicular spine; (f): putative female condition of sexual dimorphic character; LTAS: lateral terminal accessory spine; LTS: lateral terminal spine; LV: lateroventral; MD: middorsal; MSW-6: Maximum sternal width, measured on segment 6 in this species; S: segment lengths; SW-10: standard width, always measured on segment 10; TL: trunk length. Dash –: indicates that the structure could not be measured.

Character	Length Holotype	Length KIN-536	Length KIN-537
TL	279 µm	295 µm	299 µm
MSW-6	49 µm	50 µm	–
MSW-6/TL	17.6%	16.9%	–
SW-10	39 µm	40 µm	–
SW-10/TL	14.0%	13.6%	–
S1	28 µm	28 µm	29 µm
S2	28 µm	28 µm	28 µm
S3	33 µm	29 µm	33 µm
S4	32 µm	30 µm	40 µm
S5	33 µm	34 µm	41 µm
S6	34 µm	34 µm	44 µm
S7	38 µm	37 µm	45 µm
S8	43 µm	39 µm	44 µm
S9	40 µm	37 µm	42 µm
S10	38 µm	37 µm	37 µm
S11	52 µm	48 µm	48 µm
MD4 (ac)	broken	27 µm	30 µm
MD5 (ac)	broken	35 µm	42 µm
MD6 (ac)	broken	46 µm	52 µm
MD7 (ac)	broken	57 µm	61 µm
MD8 (ac)	broken	68 µm	74 µm
LV6 (ac)	broken	26 µm	30 µm
LV7 (ac)	broken	33 µm	36 µm
LV8 (ac)	broken	40 µm	42 µm
LV9 (ac)	36 µm	37 µm	39 µm
LTS	73 µm	66 µm	66 µm
LTS/TL	26.2%	22.4%	22.1%
LTAS (f)	43 µm	broken	32 µm

TABLE 4. Summary of nature and location of sensory spots, glandular cell outlets and spines arranged by series in *Echinoderes cernunnos* **sp. nov.** from the Korean South Sea. Abbreviations: LA: Lateral accessory; LD: laterodorsal; LV: lateroventral; MD: middorsal; ML: midlateral; PD: paradorsal; PV: paraventral; SD: subdorsal; SL: sublateral; VL: ventrolateral; VM: ventromedial; ac: acicular spine; (f): female condition of sexual dimorphic character; gco1/2: glandular cell outlet type 1/2; ltas: lateral terminal accessory spine; lts: lateral terminal spine; si: sieve plate; ss: sensory spot; tu: tubule.

Position	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM	PV
Segment											
1			ss	ss						ss	
2	gco1,ss		gco2	ss,gco2,ss		gco2			gco2	ss	
3	gco1		ss		ss					gco1	
4	ac		ss							gco1	
5	ac	gco1	ss		gco2			tu		ss,gco1	
6	ac	gco1,ss	ss		ss			ac		ss	gco1
7	ac	gco1,ss	ss		gco2			ac		ss	gco1
8	ac	gco1,ss	ss			gco2		ac			gco1
9		gco1,ss	ss		ss		si	ac	ss		gco1
10	gco1,gco1		ss	tu?					ss		gco1
11		ss					ltas(f?)	lts			

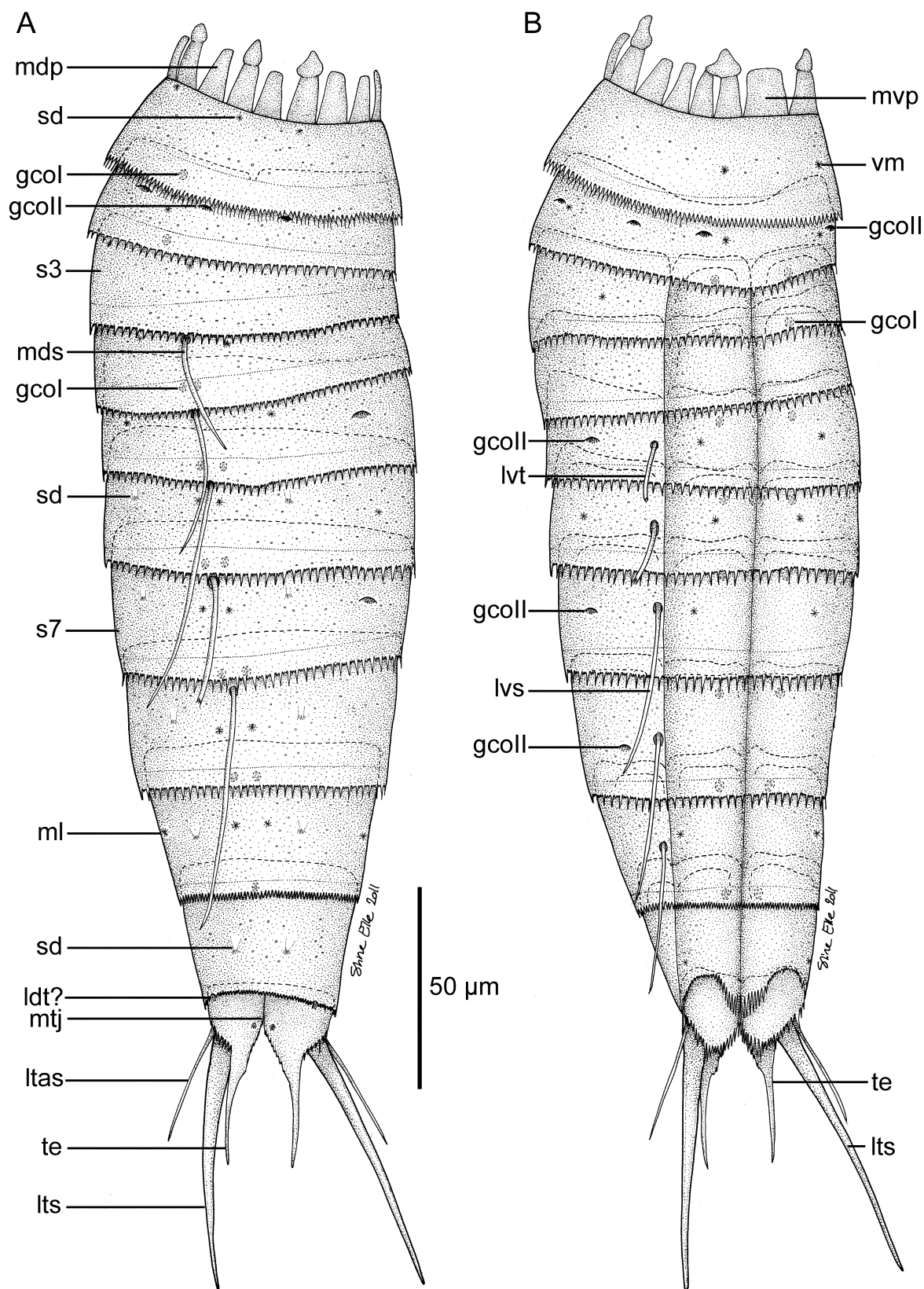


FIGURE 4. Line art illustrations showing general female habitus in *Echinoderes cernunnos* sp. nov: A, dorsal view; B, ventral view. Abbreviations: gco I/II, glandular cell outlet type 1/2; ldt?, laterodorsal tubule?; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; lvt, lateroventral tubule; mdp, middorsal placid; mds, middorsal spine; ml, midlateral sensory spot; mtj, midtergal junction;.mvp, midventral placid; s, segment followed by segment number; sd, subdorsal sensory spot; te, tergal extension; vm, ventromedial sensory spot.

Segment 2 consists of one complete cuticular ring. Pairs of conspicuous glandular cell outlets type 2 present in subdorsal, laterodorsal, sublateral and ventrolateral positions (Figs 4A–B, 5A–B, 6D). Sensory spots present as an unpaired one in middorsal position, two pairs in laterodorsal position on each side of the gco2 (Fig. 6D), and one pair in ventromedial positions; sensory spots on this and following eight segments are minute, consisting of a few papillae forming a circle around a central pore. An unpaired middorsal pore field (i.e., glandular cell outlet type 1 (gco1)) is present in middorsal position (Fig. 5A). Cuticular hairs on this and the following segments emerge through slit-like perforation sites; hairs on dorsal and lateral sides are scattered in a median belt that is limited posteriorly by the IJ-line; no hairs present on ventral side. A secondary pectinate fringe was not observed on this or any of the following segments. Posterior segment margin with regular pectinate fringe on dorsal and ventral sides, whereas the fringes on the lateral sides are composed of well-spaced long and narrow fringe tips, with much shorter tips in between.

Segment 3 and following seven segments, down to segment 10, consist of one tergal and two sternal plates (Fig. 4B). On all segments with this composition, pachycycli are well-developed along anterior margins of the sternal plates, and along anterior 1/3 of tergo-sternal and midsternal junctions. Segment with sensory spots in subdorsal and midlateral positions, and unpaired middorsal and paired ventromedial pore fields (gco1). Cuticular hairs scattered in a median belt around the tergal plate and onto the ventrolateral areas of the sternal plates; no cuticular hairs in ventromedial and paraventral areas. Posterior segment margin as lateral margin on preceding segment.

Segment 4 with middorsal spine (Fig. 4A). One pair of sensory spots present in subdorsal position. Pore fields (gco1) in ventromedial positions (Fig. 4B). Cuticular hairs and pectinate fringe as on preceding segment.

Segment 5 with middorsal spine and lateroventral tubules (length = 13 μ m, estimated with SEM) (Figs 4A–B). Paired paradorsal pore fields (gco1) present, anterior to the attachment point of the middorsal spine (Figs 4A, 5C); one additional pair present in ventromedial position. One pair of conspicuous glandular cell outlets type 2 present in midlateral positions (Figs 4B, 5C). Sensory spots present in subdorsal and ventromedial positions; subdorsal sensory spots with short, tube-shaped subcuticular structure (Fig. 5D). Cuticular hairs and pectinate fringe as on preceding segment.

Segment 6 with middorsal spine and lateroventral spines (Figs 4A–B, 5C, 6E). Paired pore fields (gco1) present slightly anterior to attachment point of the middorsal spine (Fig. 5C); one additional pair present in paraventral position. Sensory spots present in paradorsal, subdorsal, midlateral (Fig. 5C) and ventromedial positions; paradorsal ones are very close to the subdorsal area, and do not readily appear as perispinal sensory spots; subdorsal sensory spots with tube-shaped subcuticular structure (Fig. 5D); ventromedial ones located slightly closer to the midsternal line than those on the preceding segment. Cuticular hairs and pectinate fringe as on preceding segment.

Segment 7 with middorsal spine and lateroventral spines. Paired pore fields (gco1) present slightly anterior to attachment point of the middorsal spine (Figs 4A, 5C); one additional pair present in paraventral position. One pair of conspicuous glandular cell outlets type 2 present in midlateral positions (Figs 4B, 5C, 6E). Sensory spots present in paradorsal (as on preceding segment), subdorsal and ventromedial positions; subdorsal sensory spots with tube-shaped subcuticular structure; ventromedial ones located slightly more lateral than those on the preceding segment. Cuticular hairs and pectinate fringe as on preceding segment.

Segment 8 with middorsal spine and lateroventral spines. Paired pore fields (gco1) present slightly anterior to attachment point of the middorsal spine; one additional pair present in paraventral position. One pair of conspicuous glandular cell outlets type 2 present in sublateral positions (Fig. 4B). Sensory spots present in paradorsal (as on preceding segment) and subdorsal positions; subdorsal sensory spots with tube-shaped subcuticular structure. Cuticular hairs and pectinate fringe as on preceding segment.

Segment 9 without middorsal spine, but with lateroventral spines. Paired pore fields (gco1) present in paradorsal and paraventral positions; paraventral pore fields closer to midsternal line than those on preceding segments. Sensory spots present in paradorsal (as on preceding segment), subdorsal, midlateral and ventromedial positions; subcuticular structures associated with subdorsal sensory spots are anteriorly expanded, giving them a funnel-shaped rather than tube-shaped appearance (Fig. 5E). Small, rounded sieve plates present in lateral accessory positions. Cuticular hairs as on preceding segment, but almost lacking in mid- and paradorsal areas. Pectinate fringe with uniform, well-developed fringe tips around the segment margin.

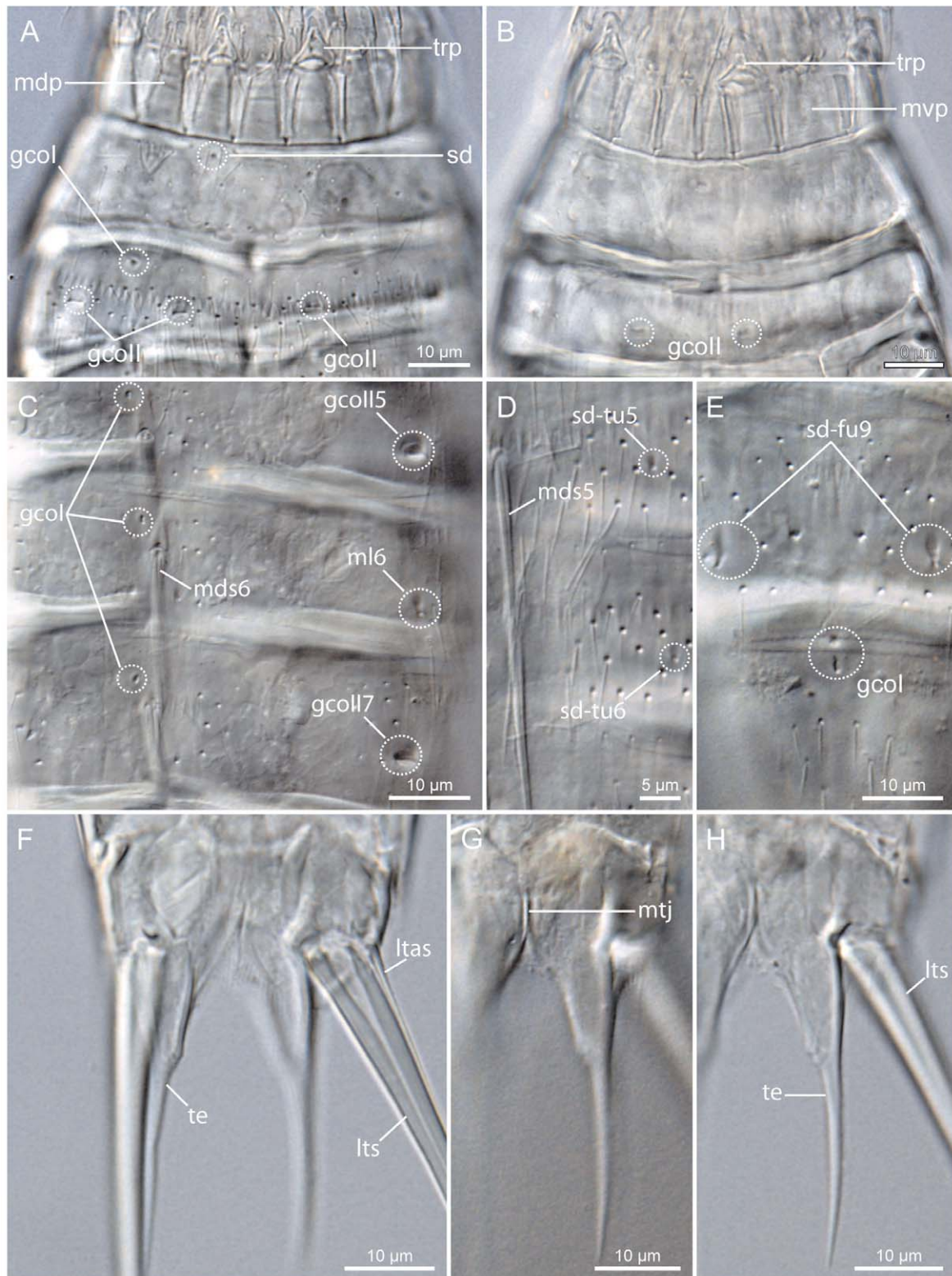


FIGURE 5. Light micrographs showing details in neck and trunk morphology of the female holotype of *Echinoderes cernunnos* sp. nov., NIBR Acc. No. INBRIV0000245082: A, neck and segments 1 and 2, dorsal view; B, neck and segments 1 and 2, ventral view; C, Segments 5 to 7, middorsal to midlateral regions on right half of tergal plates; D, segments 5 and 6, close-up of middorsal to subdorsal regions on right half of tergal plates; E, segments 9 and 10, close-up of middorsal and subdorsal areas; F, segment 11, focused on left side tergal extension and terminal spines; G, segment 11, focused on midtergal junction; H, segment 11, focused on right side tergal extension. Abbreviations: gco I/II, glandular cell outlet type 1/2; ltas, lateral terminal accessory spine; lts, lateral terminal spine; mdp, middorsal placid; mds, middorsal spine; ml, midlateral sensory spot; mtj, midtergal junction; mvvp, midventral placid; sd (tu/fu), subdorsal sensory spot (with tube-shaped/funnel-shaped subcuticular structure); te, tergal extension; trp, trichoscalid plate. Digits after the labels refer to the segment numbers.

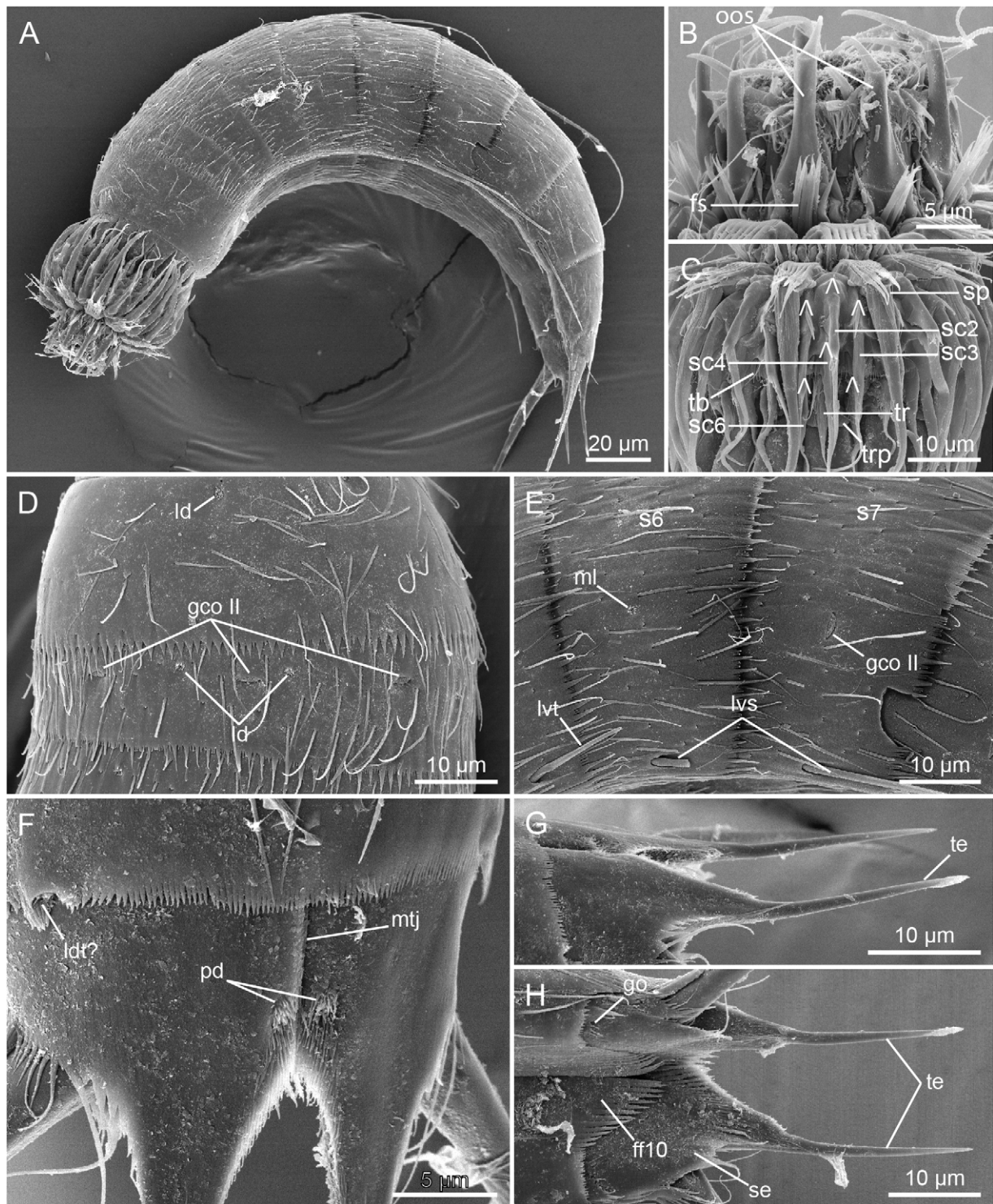


FIGURE 6. Scanning electron micrographs showing overviews and details in head and trunk morphology of female *Echinoderes cernunnos* **sp. nov.**: A, lateral overview of whole specimen; B, detail of head, showing partly extended mouth cone and outer oral styles; C, detail of head showing introvert section 8; D, segments 1 and 2, dorsolateral view; E, segments 6 and 7, midlateral view; F, segment 11, subdorsal view; G, segment 11, lateral view; H, segment 11, ventral view. Abbreviations: ff, free flap, fs, fringe of style basis; gco II, glandular cell outlet type 2; go, gonopore; ld, laterodorsal sensory spot; ldt?, laterodorsal tubule?; lvs, lateroventral spine; lvt, lateroventral tubule; ml, midlateral sensory spot; mtj, midtergal junction; oos, outer oral styles; pd, paradorsal sensory spot; sc, scalids; se, sternal extension; sp, spinoscalids; tb, transverse band of ridges; te, tergal extension; tr, trichoscalid; trp, trichoscalid plate. Digits after labels refer to the introvert ring numbers on C, otherwise to segment number. Lambda symbols Λ mark attachment point of scalids.

Segment 10 without spines. Two unpaired, middorsal pore fields (gco1) (Fig. 5E) and paired paraventral ones present; paraventral pore fields closer to midsternal line than those on preceding segments. Sensory spots with funnel-shaped subcuticular structure present in subdorsal positions; a regular pair of sensory spots present in ventrolateral position. A pair of fringed tufts extends slightly beyond the posterior segment margin in the laterodorsal position; the structures could be very short tubules with fringed tips, but this is uncertain (structure marked as “ldt?” on Figs 4A, 6F). Cuticular hairs scattered in middorsal, laterodorsal and lateroventral/ventrolateral clusters. Posterior segment margin with pectinate fringe; fringe tips short along dorsal margin, and along the lateral ones; paraventrally the sternal plates and the fringe tips are elongated, almost reaching the margin of segment 11 (Figs 4B, 6H).

Segment 11 is composed of two tergal and two sternal plates (Figs 4A–B, 5G, 6F). Lateral terminal spines and lateral terminal accessory spines present (Figs 4A–B, 5F); the latter is probably a sexually dimorphic female trait, but male specimens were unavailable to confirm this. Sensory spots present in paradorsal position (Fig. 6F). Cuticular hairs not present. Tergal extensions extremely elongated and posteriorly projecting (Figs 4A, 5F–H, 6G–H), measuring 38 μm and constituting 70% of the total segment length; sternal extensions short and rounded with fringed margins and a few longer filiform extensions (Figs 4B, 6H).

Notes on diagnostic features and affinities. Even though *Echinoderes cernunnos* **sp. nov.** displays a rather classic spine pattern, with five middorsal spines and lateroventral spines/tubules on segments 5 to 9, the species possesses several unique traits that make it impossible to confuse with any other taxon. Also the lack of ventrolateral tubules is uncommon, and only shared with a minority of its congeners. The most prominent characteristic, however, is its extremely elongated tergal extensions. Their lengths clearly exceed tergal extensions in any other species, inclusive those in *E. higginsi* Huys & Coomans, 1989 and *E. spinifurca* Sørensen, Heiner & Ziemer, 2005 that otherwise possess the longest tergal extensions among the species known so far (see Huys & Coomans 1989; Sørensen *et al.* 2005). As stated above, the tergal extensions of *E. cernunnos* **sp. nov.** constitute 70% of the total segment length, whereas the corresponding ratios in *E. higginsi* and *E. spinifurca* are about 50% only.

Also the distribution of glandular cell outlets type 2 (gco2) appears to be unique for this species. Our information about the presence and distribution of gco2 is still quite limited, because previous descriptions have tended to neglect this character. However, to our knowledge, no other species displays the specific pattern of gco2 as the one found in *E. cernunnos* **sp. nov.**

The third character that attracts special attention and makes *E. cernunnos* **sp. nov.** unique among congeners is the middorsal division of segment 11 that splits the tergal plate into two paired plates. No other species of the genus has this segment composition, and it inevitably makes the generic assignment of the species problematic. Among the five genera of Echinoderidae, *Cephalorhyncha* Adrianov, 1999 in Adrianov & Malakhov, 1999, *Fissuroderes* Neuhaus & Blasche, 2006 and *Meristoderes* Herranz *et al.*, 2012 accommodate species with middorsally split tergal plate on segment 11 (Neuhaus & Blasche, 2006; for *Meristoderes* Sørensen pers. obs. from yet undescribed species). However, these genera are characterized by species with either fully or at least partly differentiated sternal plates on segment 2 (Adrianov & Malakhov 1999; Neuhaus & Blasche 2006; Herranz *et al.* 2012). Segment 2 in *E. cernunnos* **sp. nov.** is composed of a closed cuticular ring, which characterizes species of *Echinoderes*, hence we tentatively assign the species to this genus. The conflicting characters could indicate that a future reassignment could be required, and in any case, this character combination clearly makes *E. cernunnos* **sp. nov.** special among all echinoderids.

***Echinoderes microaperturus* sp. nov.**

(Figures 7–10, Tables 5–6)

Diagnosis. Specimens with middorsal spines on segments 4 to 8, not extending beyond the posterior margin of their respective segments; ventrolateral tubules on segment 2; lateroventral tubules on segment 5; lateroventral spines on segments 6 to 9; midlateral tubules on segment 10. Minute glandular cell outlets type 2 subdorsal on segment 2 and laterodorsal on segments 8 and 9. Females with glands with funnel-shaped subcuticular structure ventrolateral on segment 7 and ventromedial on segment 8. Tergal extensions of segment 11 long, spinose. Lateral terminal spines 69–81% of trunk length.

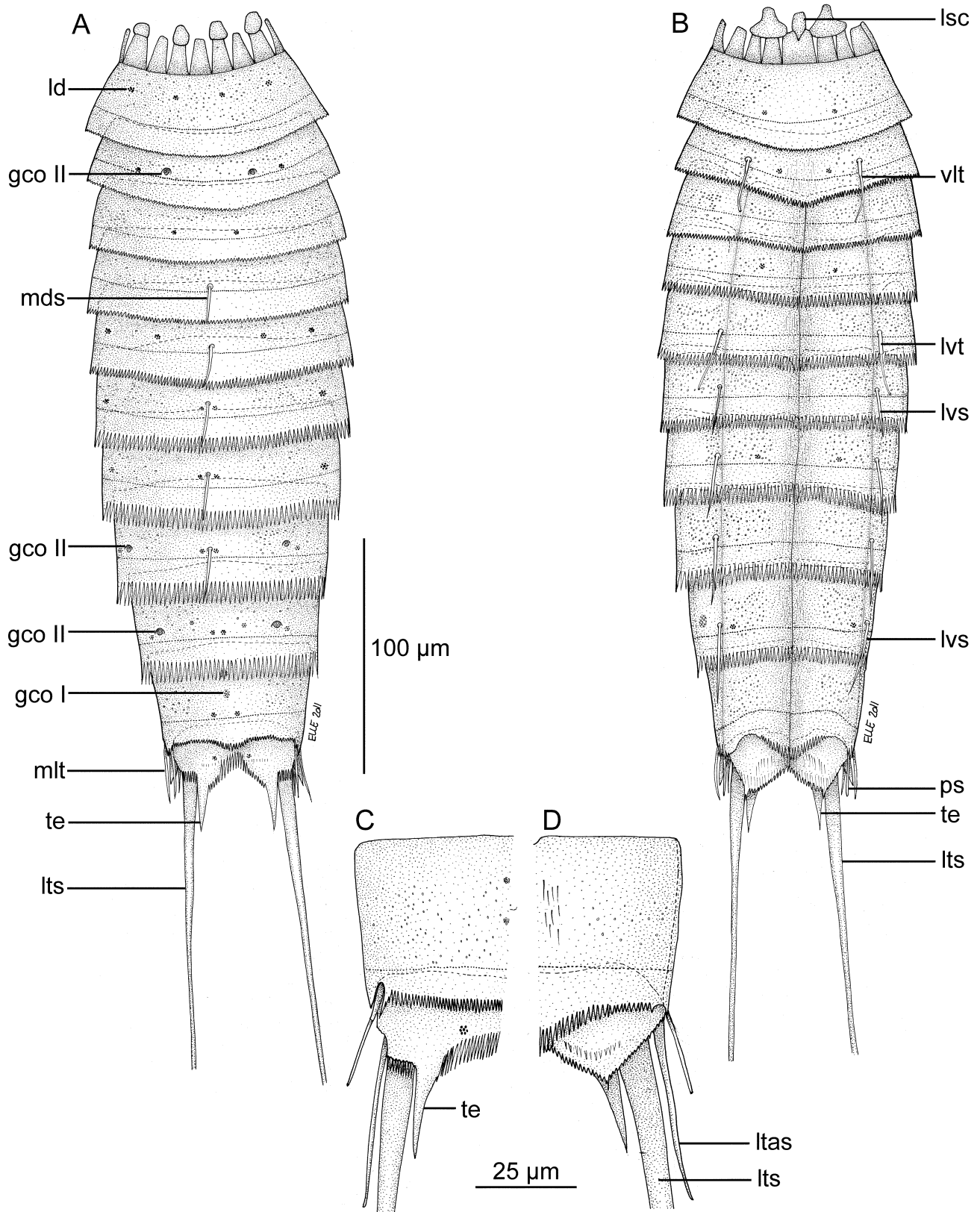


FIGURE 7. Line art illustrations showing general habitus and sexual dimorphism in *Echinoderes microaperturus* **sp. nov.**: A, male, dorsal view; B, male, ventral view; C, segments 10 and 11 in female, dorsal view; D, segments 10 and 11 in female, ventral view. Abbreviations: gco I/II, glandular cell outlet type 1/2; ld, laterodorsal sensory spot; lsc, leaf-like scolid; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvt, lateroventral tubule; lvs, lateroventral spine; mds, middorsal spine; mlt, midlateral tubule; ps, penile spines; te, tergal extension; vlt, ventrolateral tubule.

Type material. Holotype adult male collected on 6 June 2008 from station MAP-08 in the Korea Strait, ca. 100 km south of Jeju Island, (Fig. 1C), 32°21.59'N 126°46.32'E, from mud at 113 m depth, mounted in Fluoromount G, deposited at NIBR under accession number INBRIV0000245083. Allotype adult female collected on 6 August 2008 from station MAP-24 in the East China Sea, ca. 325 km southwest of Jeju Island, (Fig. 1C), 30°19.86'N 125°17.06'E, from mud at 74 m depth, mounted in Fluoromount G, deposited at NHMD under accession number ZMUC KIN-539. Paratypes: five specimens (two females and three males) from the same locality as holotype; two specimens (a female and a male) from same locality as allotype; and two males collected on 28 September 2006 from station MAP-05 in the East China Sea, ca. 300 km south of Jeju Island, (Fig. 1C), 30°31.66'N 125°55.86'E, from mud at 79 m depth; all paratypes mounted in Fluoromount G, deposited at NHMD under accession number ZMUC KIN-540 to KIN-548.

Additional material. Mounted for SEM and stored in personal collection of MVS, originated from stations MAP-05 and MAP-08 (mentioned above), as well as stations MAP-07 and MAP-27 (see Fig. 1C and Table 1). Four additional specimens, mounted in Fluoromount G, are stored in the personal collections of HSR and CYC.

Etymology. The species name *microaperturus* refers to the minute openings of the glandular cell outlets type 2 that make it easy to recognize the species.

Description. Adult specimens consist of a head, a neck and eleven trunk segments (Figs 7A–B, 10A). Measurements and dimensions are given in Table 5. A summary of sensory spot, spine, tubule and glandular cell outlet positions is provided in Table 6.

TABLE 5. Measurements of adult *Echinoderes microaperturus* sp. nov. from the Korea Strait and East China Sea (Stations: MAP-08 and MAP-24), including number of measured specimens (n) and standard deviation (S.D.). Abbreviations: (ac): acicular spine; (f): female condition of sexual dimorphic character; LTAS: lateral terminal accessory spine; LTS: lateral terminal spine; LV: lateroventral; MD: middorsal; ML: midlateral; MSW-7: Maximum sternal width, measured on segment 7 in this species; S: segment lengths; SW-10: standard width, always measured on segment 10; TL: trunk length; (tu): tubule; VL: ventrolateral.

Character	n	Range	Mean	S.D.
TL	10	263 – 313 µm	278 µm	14.02 µm
MSW-7	10	57 – 63 µm	60 µm	2.45 µm
MSW-7/TL	10	19.5 – 23.2%	21.7%	1.17%
SW-10	10	51 – 61 µm	57 µm	3.29 µm
SW-10/TL	10	18.5 – 22.1%	20.4%	1.46%
S1	10	27 – 30 µm	29 µm	1.16 µm
S2	10	26 – 30 µm	28 µm	1.26 µm
S3	10	27 – 33 µm	29 µm	1.73 µm
S4	10	30 – 34 µm	32 µm	1.43 µm
S5	10	34 – 37 µm	36 µm	1.25 µm
S6	10	37 – 40 µm	38 µm	0.95 µm
S7	10	38 – 41 µm	40 µm	1.07 µm
S8	10	40 – 43 µm	42 µm	1.14 µm
S9	10	41 – 44 µm	43 µm	1.20 µm
S10	10	37 – 43 µm	41 µm	2.32 µm
S11	10	38 – 40 µm	39 µm	0.79 µm
MD 4 (ac)	8	11 – 15 µm	13 µm	1.25 µm
MD 5 (ac)	8	13 – 16 µm	15 µm	1.13 µm
MD 6 (ac)	9	14 – 18 µm	16 µm	1.41 µm
MD 7 (ac)	9	15 – 20 µm	18 µm	1.54 µm
MD 8 (ac)	9	21 – 25 µm	22 µm	1.32 µm
VL 2 (tu)	5	16 – 24 µm	20 µm	3.16 µm
LV 6 (ac)	10	15 – 21 µm	18 µm	1.81 µm
LV 7 (ac)	10	16 – 26 µm	23 µm	1.96 µm
LV 8 (ac)	9	22 – 26 µm	25 µm	1.59 µm
LV9 (ac)	8	27 – 31 µm	29 µm	1.25 µm
ML 10 (tu)	10	22 – 28 µm	24 µm	2.01 µm
LTS	9	210 – 219 µm	215 µm	3.35 µm
LTS/TL	9	69.3 – 81.4%	77.1%	3.54 %
LTAS (f)	5	35 – 45 µm	40 µm	4.16 µm

TABLE 6. Summary of nature and location of sensory spots, glandular cell outlets and spines arranged by series in *Echinoderes microaperturus* **sp. nov.** Abbreviations: LA: Lateral accessory; LD: laterodorsal; LV: lateroventral; MD: middorsal; ML: midlateral; PD: paradorsal; SD: subdorsal; VL: ventrolateral; VM: ventromedial; ac: acicular spine; (f): female condition of sexual dimorphic character; gco1/2: glandular cell outlet type 1/2; gfs: gland with funnel-shaped subcuticular structure; ltas: lateral terminal accessory spine; lts: lateral terminal spine; si: sieve plate; ss: sensory spot; tu: tubule.

Position Segment	MD	PD	SD	LD	ML	LA	LV	VL	VM
1			ss	ss	ss				ss
2			gco2	ss				tu	ss
3			ss						
4	ac								ss
5	ac		ss	ss			tu		
6	ac	ss		ss			ac		
7	ac	ss		ss			ac	gfs (f)	ss
8	ac	ss		gco2,ss			ac		gfs (f)
9		ss	ss	gco2,ss		si	ac	ss	
10	gco1,gco1		ss		tu				
11			ss			ltas (f)	lts		

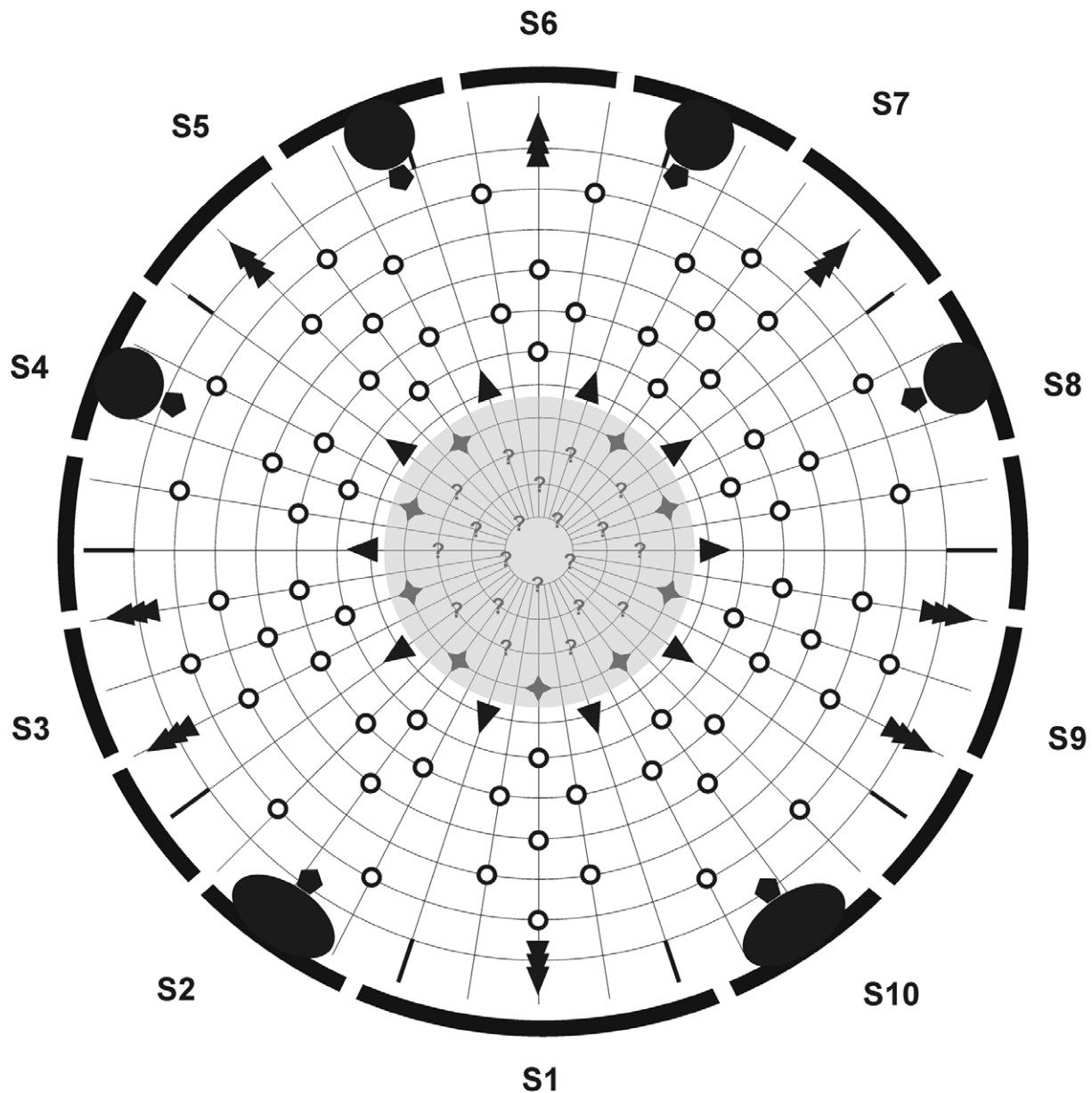
The head consists of a retractable mouth cone and an introvert (Figs 8, 10B–C). Inner armature in mouth cone could not be examined. Outer armature with nine outer oral styles composed of two subunits. Bases of outer oral styles with ornamented double rows of fringes; inner fringe rows with several, rather short fringe tips; outer fringe rows with 6 to 8 much longer and more slender fringe tips (Fig. 10C). Introvert with 10 spinoscalids in ring 1, followed by 10, 20 and 10 scalids, respectively, in rings 02 to 04. Ring 05 with 10 scalids, arranged as two scalids in each uneven numbered section; and ring 06 with 15 scalids, arranged as one scalid in each uneven numbered section and two scalids in each even numbered one. Hence, described section-wise, uneven numbered sections have seven regular scalids, whereas even numbered ones have six (Figs 8, 10B). Additional scalids are present in ring 07. These resemble an intermediate between regular scalids and trichoscalids. Their bases are broad with fringed lateral edges, which give the bases a leaf-like appearance, hence, these scalids will be referred to as leaf-like scalids. Leaf-like scalids do not follow a strict pentaradial distribution, but are present as one scalid in sections 1 (Fig. 9B), 5, 6 and 7, and two scalids in sections 3 and 9 (Figs 8, 10B).

The neck consists of 16 placids (Fig. 8), all measuring 13 µm in length and 7 µm in width at bases (Figs 7A, 9A), except midventral placid that measures 12 µm in width (Figs 7B, 9B). Placids in positions corresponding to introvert sections 2 and 10 with broad trichoscalid plate with attached trichoscalid (Figs 7B, 8, 9B). Smaller trichoscalid plates with trichoscalids associated with placids in positions corresponding to introvert sections 2, 5, 7 and 8 (Figs 7A, 8, 9A).

Segment 1 consists of one complete cuticular ring. Pairs of subdorsal, laterodorsal, midlateral and ventromedial sensory spots present (Figs 7A–B, 9A–B). Sensory spots on this, and all following segments, are generally small (ca. 1 µm in diameter) and rounded. Pore fields were not observed. Cuticular hairs on this and following segments emerge through slit-like perforation sites (unless other is mentioned). Hairs are scattered on all sides of the segment, from anterior margin to IJ-line. Posterior margin with short, but well-developed pectinate fringe; fringe tips become progressively longer on each segment towards segment 8 and 9.

Segment 2 consists of one complete cuticular ring with pair of ventrolateral tubules (Figs 7B, 9B). Pairs of laterodorsal and ventromedial sensory spots present. A pair of small (opening ca. 0.8 µm) glandular cell outlets type 2 present in the subdorsal position (Figs 7A, 9A). Cuticular hairs scattered over tergal plate and in ventrolateral positions of sternal plates. Narrow, elongate clusters of filiform cuticular projections are present in the paraventral positions.

Segment 3 and following eight segments consist of one tergal and two sternal plates. All segments with this composition have well-developed pachycycli along anterior segment margins, and along anterior 1/3 of tergo-sternal and midsternal junctions. Paired sensory spots located in subdorsal position (Fig. 7A). Cuticular hairs are scattered all over the tergal plate, except in a small hairless laterodorsal patches on the anterior part of the segment. Cuticular hairs and filiform extensions on sternal plates as on preceding segment.



Scalid and style arrangement

By ring:

Ring -01 to -03: ?
 Ring 00: 9 outer oral styles
 Ring 01: 10 spinoscalids
 Ring 02: 10 scalids
 Ring 03: 20 scalids
 Ring 04: 10 scalids
 Ring 05: 10 scalids
 Ring 06: 15 scalids

Ring 07: 8 leaf-like scalids

Trichoscalid row: 14 trichoscalids

By section:

Uneven sections: 7 scalids (+1 or 2 leaf-like scalids)

Even sections: 6 scalids (+1 leaf-like scalid in sec. 6)

FIGURE 8. Diagram of mouth cone (grey shaded area), introvert and placids in *Echinoderes microaperturus* **sp. nov.** with indication of inner and outer oral styles, scalid and placid distribution. Placids and trichoscalid plates are symbolized by the black-shaded bent bars and circles around the introvert diagram.

Segment 4 with short middorsal spine and ventromedial sensory spots (Fig. 7A–B). Cuticular hairs and filiform extensions as on preceding segment.

Segment 5 with short middorsal spine and lateroventral tubules (Fig. 7A–B). Length of lateroventral tubes could not be measured exactly with LM, but from SEM observations they are estimated to be about same length as lateroventral spines on segment 6, hence, ca. 15 to 20 μm . Pairs of subdorsal and laterodorsal sensory spots present. Cuticular hairs and filiform extensions as on preceding segment.

Segments 6, 7 and 8 with short middorsal spine and lateroventral spines (Fig. 7A–B). Pairs of paradorsal and laterodorsal sensory spots present. Cuticular hairs and filiform extensions as on segment 5. Segment 7 furthermore with pair of minute (0.8 μm), ventromedial sensory spots, and segment 8 with pair of small (opening ca. 0.8 μm) glandular cell outlets type 2 in the laterodorsal position (Figs 7A, 9C, 10D). Females with paired glands with funnel-shaped subcuticular structure in ventrolateral positions of segment 7 (Fig. 9D) and ventromedial positions of segment 8 (Fig. 9E). Cuticular hairs and filiform extensions as on preceding segment.

Segment 9 without middorsal spine, but with spines in the lateroventral position. Pairs of paradorsal, subdorsal, laterodorsal and ventrolateral sensory spots present (Fig. 7A–B). A pair of small (opening ca. 0.8 μm) glandular cell outlets type 2 is present in the laterodorsal position (Figs 7A, 9C, 10D), and minute (ca. 3 μm in diameter), rounded sieve plates in lateral accessory position. Cuticular hairs and filiform extensions as on preceding segment.

Segment 10 without acicular spines, but with pair of midlateral tubules that emerge from deep incisions in the posterior segment margin (Figs 7A, 9C, 10E–G). Sensory spots present in the subdorsal positions only. Two middorsal glandular cell outlets type 1 (pore fields) are present on the anterior part of the segment; anteriormost outlet may be covered by pectinate fringe of preceding segment (Fig. 9C). Cuticular hairs and filiform extensions as on preceding segment. Pectinate fringe of posterior segment margin much shorter than on preceding segments.

Segment 11 with lateral terminal spines. Females furthermore with lateral terminal accessory spines (Figs 7C–D, 9F, 10E, G), and males with three pairs of penile spines that emerge from the intersegmental joint with the preceding segment (Figs 7A–B, 10F, H). The dorsal- and ventralmost penile spines are long and flexible, whereas the median one is shorter and stouter. A pair of sensory spots is present in the subdorsal position. Cuticular hairs are not present, but a cluster of cuticular filiform extensions covers the mid- to subdorsal positions of the posterior part of the tergal plate (Figs 7A, 10E–F). Similar extensions form a transverse band on the sternal plates (Figs 7B, 10G–H). A thin pectinate fringe is present along the posterior margins of the sternal plates, and along the attachment site of the lateral terminal spines. Tergal plate terminates into spinous extensions (Figs 7A–C, 9F, 10E–H), whereas sternal plates terminate along an oblique margin that never extends beyond the tergal plate (Figs 7B–D, 10H).

Notes on diagnostic features. *Echinoderes microaperturus* **sp. nov.** is most easily recognized by the pattern of its rather short acicular spines, combined with the presence of long, spinous tergal extensions of segment 11, the small glandular cell outlets type 2 in subdorsal position on segment 2 and in laterodorsal positions on segments 8 and 9.

The spine pattern, i.e., middorsal spines on segments 4 to 8, ventrolateral tubules on segment 2, lateroventral spines/tubules on segments 5 to 9, and laterodorsal/midlateral tubules on segment 10, is among the most common ones within the genus and has previously been reported from 19 species (see Thormar & Sørensen 2010). However, *Echinoderes microaperturus* **sp. nov.** can quite easily be distinguished from 11 of the 19 species by its rather short middorsal spines that hardly extend beyond the posterior margin of the segments to which they are attached. Oppositely, the middorsal spines (at least those on the more posterior segments) in the 11 species always extend well beyond their segments. Of the remaining eight species, four also differ significantly from *E. microaperturus* **sp. nov.**: *Echinoderes brevicaudatus* (Higgins, 1966) and *E. cavernus* Sørensen, Jørgensen & Boesgaard, 2000 are easily recognized by their conspicuously short and stout lateral terminal spines (see Higgins 1966; Sørensen *et al.* 2000), *E. imperforatus* Higgins, 1983 is unique in its complete lack of perforation sites (see Higgins 1983), and *E. truncatus* Higgins, 1983 in its very prominent perforation sites and almost truncate tergal and sternal extensions of segment 11 (see Higgins 1983).

The four species that most easily can be confused with *E. microaperturus* **sp. nov.** include *E. ehlersi* Zelinka 1913, *E. aureus*, *E. sensibilis* and *E. lanceolatus*. All four species are known from Asia, and especially the three latter have distributions that quite likely could be overlapping with *E. microaperturus* **sp. nov.**

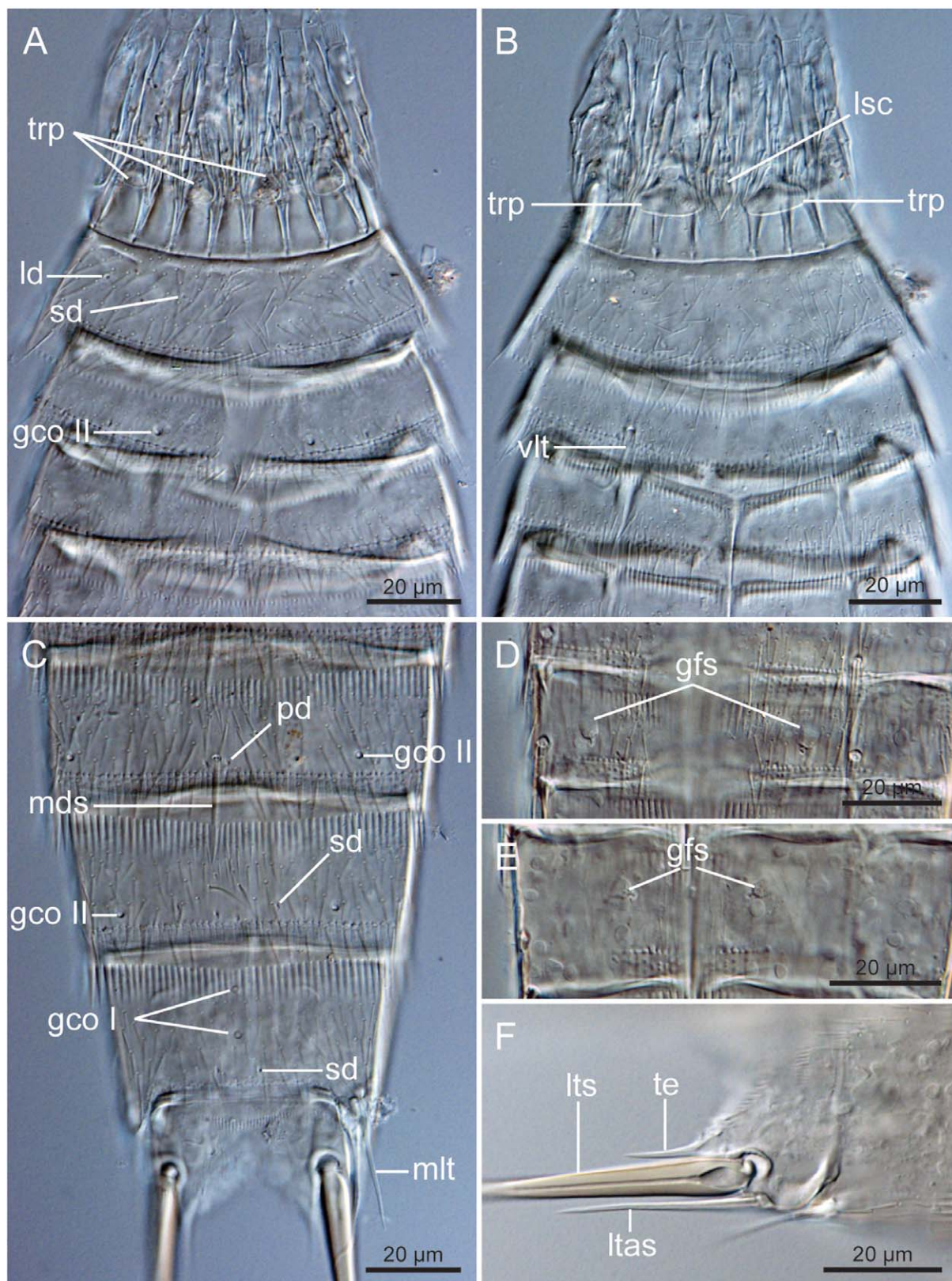


FIGURE 9. Light micrographs showing details in neck and trunk morphology of *Echinoderes microaperturus* **sp. nov.**, displaying male holotype, NIBR Acc. No. INBRIV0000245083. (A–C), female paratype, ZMUC KIN-540 (D–E), and female paratype, ZMUC KIN-541 (F): A, introvert, neck and segments 1 to 4, dorsal view; B, introvert, neck and segments 1 to 4, ventral view; C, segments 8 to 11, dorsal view; D, segment 7 in female, ventral view; E, segment 8 in female, ventral view; F, segments 10 to 11 and terminal spines in female, dorsal view. Abbreviations: gco I/II, glandular cell outlet type 1/2; gfs, gland with funnel-shaped subcuticular structure; ld, laterodorsal sensory spot; lsc, leaf-like scalid; ltas, lateral terminal accessory spine; lts, lateral terminal spine; mds, middorsal spine; mlt, midlateral tubule; pd, paradorsal sensory spot; sd, subdorsal sensory spot; te, tergal extension; trp, trichoscalid plate; vlt, ventrolateral tubule.

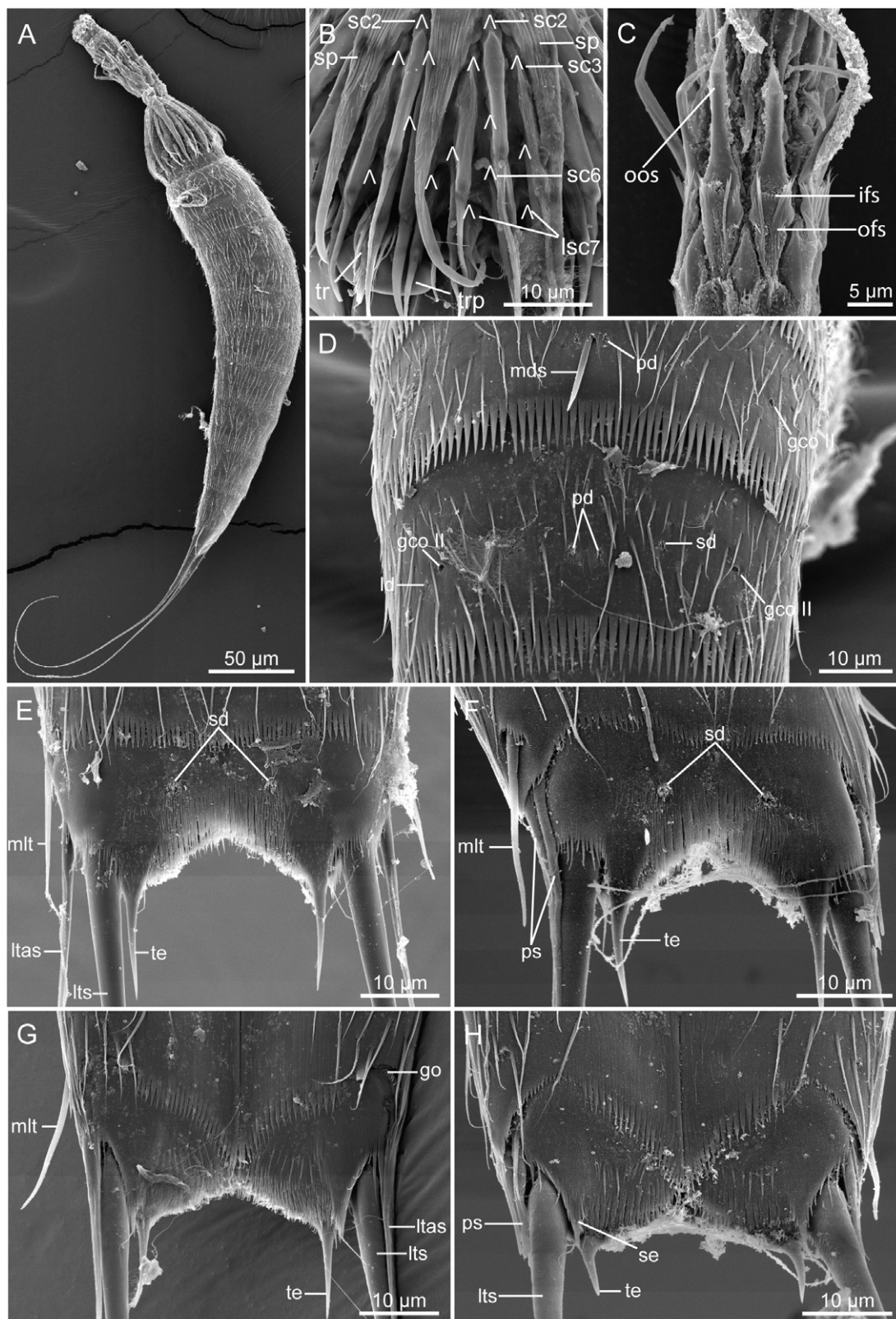


FIGURE 10. Scanning electron micrographs showing overview and details in head and trunk morphology of *Echinoderes microaperturus* **sp. nov.**: A, lateral overview of whole specimen; B, detail of head, showing introvert sections 10 (left) and 9 (right); C, detail of head showing mouth cone; D, segments 8 and 9, dorsal view; E, segments 10 to 11 in female, dorsal view; F, segments 10 to 11 in male, dorsal view; G, segments 10 to 11 in female, ventral view; H, segments 10 to 11 in male, ventral view. Abbreviations: gco II, glandular cell outlet type 2; go, gonopore; ifs, inner fringe of style basis; ld, laterodorsal sensory spot; lsc, leaf-like scalid; ltas, lateral terminal accessory spine; lts, lateral terminal spine; mds, middorsal spine; mlt, midlateral tubule; ofs, outer fringe of style basis; oos, outer oral styles; pd, paradorsal sensory spot; ps, penile spines; sc, scalids; sd, subdorsal sensory spot; se, sternal extension; sp, spinoscalids; te, tergal extension; tr, trichoscalid; trp, trichoscalid plate. Digits after the labels refer to the introvert ring numbers. Lambda symbols Λ mark attachment point of scalids.

The safest way to distinguish *E. microaperturus* **sp. nov.** is by its presence of subdorsal glandular cell outlets type 2 (gco2) on segment 2. The presence of gco2 has not been reported from any of the four species (see Zelinka 1913; Higgins & Rao 1979; Adrianov *et al.* 2002a, 2002b; Chang & Song 2002), but since this character has tended to be ignored in older contributions, its absence needs further confirmation. For *E. sensibilis*, though, it seems fair to rely on information from the description. The species' description is based on examinations with both LM and SEM, specimens examined with SEM appear very clean so that all details would have been recognizable, and the description addresses so many other cuticular details that it seems unlikely that the authors would have decided not to mention the eventual presence of gco2.

For *E. ehlersi* the situation is a bit fuzzier. The species is described from Zanzibar in West Africa by Zelinka (1913), and Higgins & Rao (1979) subsequently found it in the Andaman Islands, and address different details of its morphology. Neither Zelinka (1913) nor Higgins & Rao (1979) mention any kind of cuticular structures in the positions where *E. microaperturus* **sp. nov.** has gco2. However, the senior author recently received a few kinorhynchs from the Andaman Islands, and the specimens could readily be identified as *E. ehlersi*. A closer examination with SEM revealed though, that the specimens have tiny laterodorsal gco2 on segments 8 and 9 (M. V. Sørensen, pers. obs.). The structures were so small that they could be overlooked with LM. This leaves us with the question whether *E. ehlersi* also has laterodorsal gco2 on segments 8 and 9, which consequently would bring it very close to *E. microaperturus* **sp. nov.**, or if the examined specimens belonged to another, yet undescribed species. In any case, subdorsal gco2 were not present on segment 2, which thus makes it possible to distinguish *E. microaperturus* **sp. nov.** from its Andaman relatives.

As for *E. aureus* and *E. lanceolatus*, the situation is even more complex. Preliminary studies by the authors of the present contribution clearly indicate that *E. lanceolatus* should be considered a junior synonym of *E. aureus*, but at the same time, that some of the paratype specimens of *E. lanceolatus* are not conspecific with its holotype, and should hence be considered a new, yet undescribed species. These problems will be addressed more specifically in an upcoming contribution, but from the ongoing examinations it is clear that neither *E. aureus* nor the new species possess subdorsal gco2 on segment 2, as found in *E. microaperturus* **sp. nov.**

Another indicative character regards the relative length of the lateral terminal spines. In *E. microaperturus* **sp. nov.** the lengths of the lateral terminal spines equal to 69–81% of the trunk length, whereas this ratio is only 46–67% in *E. ehlersi*, that otherwise is the one with the longest lateral terminal spines. For the remaining three species, the ratios are even lower, namely 46% for *E. sensibilis*, and 33–43% for *E. aureus*. Other differential traits include the tergal extensions that are rather short in *E. ehlersi* and *E. sensibilis*.

In their description of *E. aureus*, Adrianov *et al.* (2002a) mention the presence of prominent subcuticular markings in a paraventral position on segment 1. We have, admittedly, had problems identifying such a structure on any of the specimens of *E. aureus* that we have examined. However, another diagnostic structure, namely the partial midventral fissure on segment 2 is most often very conspicuous, and makes it easy to distinguish between *E. aureus* and *E. microaperturus* **sp. nov.**

***Echinoderes obtuspinosus* sp. nov.**

(Figures 11–12, Tables 7–8)

Diagnosis. *Echinoderes* with middorsal spines on segments 4–8; lateroventral tubules on segment 5 and lateroventral spines on segments 6–9. Lateral terminal spines very short and stout, about 14% of trunk length. Glandular cell outlets type 2 present in subdorsal, laterodorsal, sublateral and ventrolateral positions on segment 2, in subdorsal positions on segment 4, and in sublateral position on segment 8. Segment 2 consisting of a closed cuticular ring, but with a weak indication of a midventral line.

Type material. Holotype: adult female, collected on 26 February 1999 at station CYC-26, Munseum Islet at the south coast of Jeju Island, (Fig. 1A), 33°13.52'N 126°33.92'E, Korea, found among intertidal algae, mounted in glycerine, deposited at deposited at NIBR under accession number INBRIV0000245084. No allotype designated. Paratypes: two female specimens (one rather damaged), collected on 5 November 1999 at station CYC-03, in the harbor of Geumjin on the Korean east coast, about 18 km southeast of Gangneung (Fig. 1A), 37°39.13'N 126°03.00'E, found among material washed off from a hermit crab, mounted in glycerine, deposited at NHMD under accession numbers ZMUC KIN-549 and KIN-550.

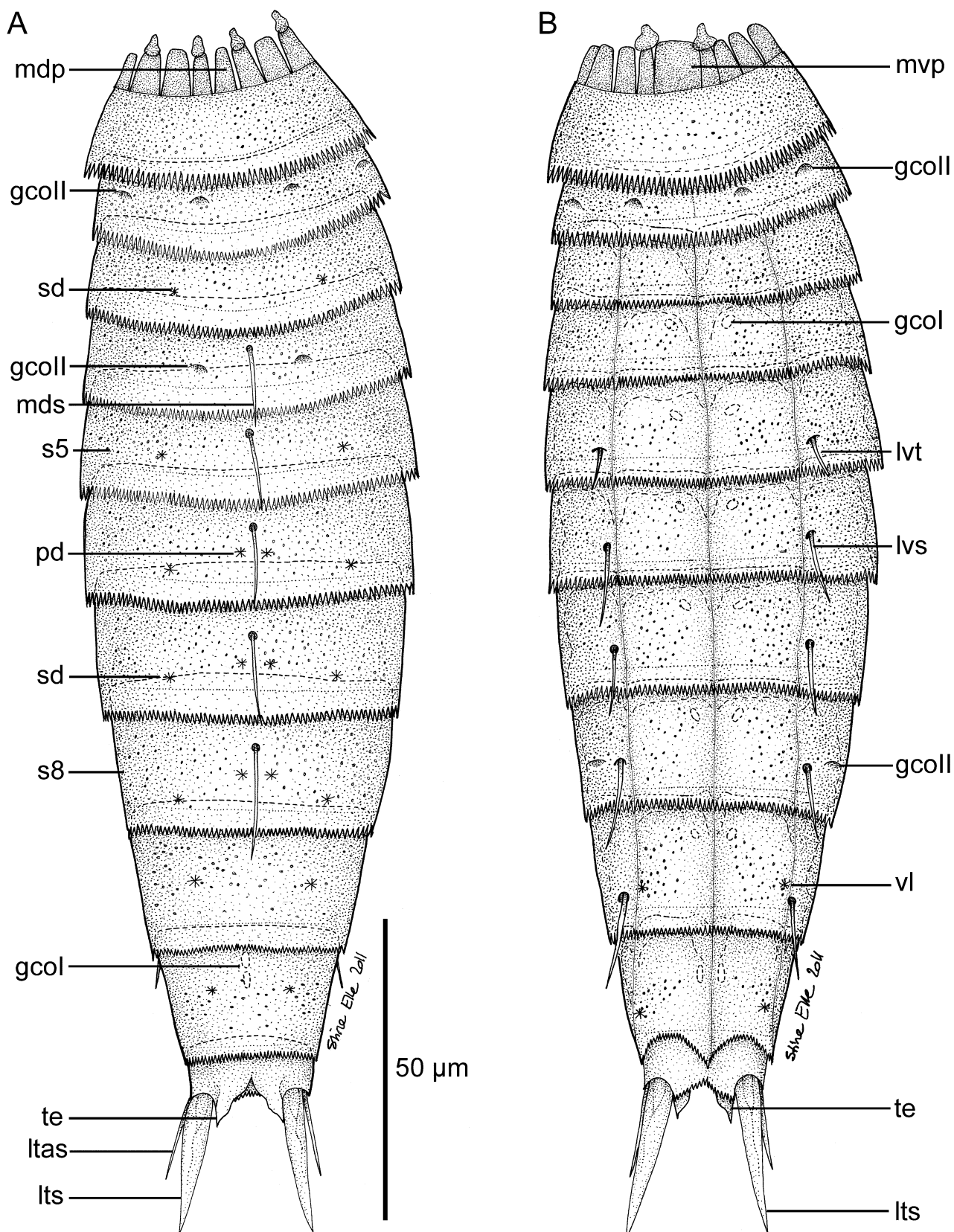


FIGURE 11. Line art illustrations showing general female habitus in *Echinoderes obtuspinosus* sp. nov.: A, dorsal view; B, ventral view. Abbreviations: gco I/II, glandular cell outlet type 1/2; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; lvt, lateroventral tubule; mdp, middorsal placid; mds, middorsal spine; mvp, midventral placid; pd, paradorsal sensory spot; s, segment followed by segment number; sd, subdorsal sensory spot; te, tergal extension; vl, ventrolateral sensory spot.

Etymology. The species name is composed of the Latin *obtus-* (thick) and *-spina* (spine), meaning the one with thick spines, with reference to the stout lateral terminal spines.

Description. Adult specimens consist of a head, a neck and eleven trunk segments (Figs 11A–B, 12E). Measurements and dimensions are given in Table 7. A summary of sensory spot, spine, tubule and glandular cell outlet positions is provided in Table 8. No specimens were available for SEM examinations, and some minor cuticular structures, especially sensory spots, could not be identified with light microscope. Hence, no mention of sensory spots in the description should not be seen as a positive confirmation of their absence.

The head consists of a retractable mouth cone and an introvert. Nine outer oral styles composed of two subunits are present. Inner armature and scalid distribution could not be examined in detail.

The neck consists of 16 placids, all measuring 15 μm in length and 9 μm in width at bases (Fig. 11A), except midventral placid that measures 12 μm in width (Fig. 11B). Placids number 2 and 16 (counting clockwise from midventral placid) with broad trichoscalid plate and attached trichoscalid. Smaller trichoscalid plates with trichoscalids on placids number 6, 8, 10, and 12.

Segment 1 consists of one complete cuticular ring (Fig. 12B). Sensory spots or pore fields could not be identified with certainty. Cuticular hairs emerge through rounded perforation sites, and are scattered all over the dorsal side of the segment, whereas those on the ventral side tend to be concentrated in a median belt that only extends towards the anterior margin in the midventral and lateroventral regions. Posterior margin with regular pectinate fringe; fringe tips clearly longest and strongest on ventral side.

Segment 2 consists of one complete cuticular ring, but with a weak indication of a midventral line (Fig. 12B). Pairs of glandular cell outlets type 2 present in subdorsal, laterodorsal, sublateral and ventrolateral positions (Figs 11A–B, 12A–B). Cuticular hairs are distributed in a median belt around the segment, limited posteriorly by the IJ-line. Posterior segment margin as on preceding segment.

Segment 3 and following eight segments consist of one tergal and two sternal plates. On all segments with this composition, pachycycli are well-developed along the anterior segment margins, and along anterior 1/3 of tergosternal and midsternal junctions. Segment with sensory spots, at least in subdorsal positions (Fig. 11A). Bracteate cuticular hairs distributed in a broad belt around the tergal plate, and in the ventrolateral and ventromedial parts of the sternal plates. Posterior segment margin with regular, well-developed pectinate fringe; fringe tips appear uniform around the segment, except in the paraventral areas where they are conspicuously shorter and thinner.

Segment 4 with middorsal spine (Fig. 11A). Cuticular markings indicate the presence of glandular cell outlets type 2 in subdorsal position (Fig. 12A). Sensory spots could not be observed, but paired pore fields (gco1) are present in ventromedial positions (Fig. 11B). Cuticular hairs and pectinate fringe as on preceding segment.

Segment 5 with middorsal spine and lateroventral tubules. Pairs of subdorsal sensory spots and ventromedial pore fields (gco1) present (Fig. 11A). Cuticular hairs and pectinate fringe as on preceding segment, except for differentiation of fringe tips in the paraventral regions that no longer appear shorter.

Segments 6 and 7 with middorsal and lateroventral spines. Sensory spots present at least in paradorsal and subdorsal positions (Figs 11A, 12C). Paired pore fields (gco1) present in ventromedial positions. Cuticular hairs and pectinate fringe as on preceding segment.

Segment 8 with middorsal and lateroventral spines. Paired glandular cell outlets type 2 present in sublateral positions (Figs 11B, 12D). Sensory spots present at least in paradorsal and subdorsal positions (Figs 11A, 12C). Paired pore fields (gco1) present in paraventral positions. Cuticular hairs and pectinate fringe as on preceding segment.

Segment 9 with lateroventral spines. Pairs of sensory spots present in subdorsal and ventrolateral positions (Fig. 12D), and pore fields (gco1) in paraventral positions. Sieve plates present in lateral accessory positions. Cuticular hairs and pectinate fringe as on preceding segment.

Segment 10 without acicular spines. Sensory spots present in the subdorsal and ventrolateral positions (Figs 11A–B). Two middorsal glandular pore fields (gco1) present on the anterior part of the segment; paired pore fields furthermore present in paraventral positions. Cuticular hairs in a middorsal patch, and a pair of lateral patches that extend into narrow, median areas on the sternal plates. Posterior segment margin of tergal plate straight, with weak pectinate fringes; sternal plates with deep ventromedial notches and a stronger fringe tips.



FIGURE 12. Light micrographs showing details in neck and trunk morphology of *Echinoderes obtuspinosus* **sp. nov.**, displaying female holotype, NIBR Acc. No. INBRIV0000245084: A, segments 2 to 4, dorsal view; B, segments 1 and 2, ventral view; C, segments 7 and 8, dorsal view; D, segments 8 and 9, ventral view; E, overview of holotype, note the LTS/TL ratio; F, segment 11 and terminal spines, with tergal extensions and LTAS in focus; G, segment 11 and terminal spines, with LTS in focus. Abbreviations: gco I/II, glandular cell outlet type 1/2; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; mds, middorsal spine; mvl, midventral line; pd, paradorsal sensory spot; te, tergal extension; vl, ventrolateral sensory spot.

Segment 11 with short and conspicuously stout lateral terminal spines (Figs 11A–B, 12F–G). Females furthermore with much thinner lateral terminal accessory spines (Fig. 12F). No males were available for examination of sexually dimorphic male characters. No sensory spots or pore fields were observed. Actual cuticular hairs emerging through perforation sites are not present. Tergal extensions are narrow, and with interrupted mesial margins (Figs 11A, 12G); sternal extensions short, oblique with dense fringes (Fig. 11B).

TABLE 7. Measurements of female holotype and two female paratypes of *Echinoderes obtuspinosus* **sp. nov.** from the Korean east coast (CYC-03) and Jeju Island (CYC-26). Abbreviations: (ac): acicular spine; (f): putative female condition of sexual dimorphic character; (tu): tubule; LTAS: lateral terminal accessory spine; LTS: lateral terminal spine; LV: lateroventral; MD: middorsal; MSW-7: Maximum sternal width, measured on segment 7 in this species; S: segment lengths; SW-10: standard width, always measured on segment 10; TL: trunk length.

Character	Length Holotype	Length Paratype KIN-549	Length Paratype KIN-550
TL	341 µm	357 µm	damaged
MSW-7	61 µm	62 µm	damaged
MSW-7/TL	17.9%	17.4%	N/A
SW-10	49 µm	52 µm	52 µm
SW-10/TL	14.4%	14.6%	N/A
S1	32 µm	35 µm	34 µm
S2	32 µm	33 µm	32 µm
S3	36 µm	35 µm	35 µm
S4	39 µm	38 µm	41 µm
S5	43 µm	43 µm	damaged
S6	44 µm	47 µm	damaged
S7	48 µm	48 µm	48 µm
S8	50 µm	51 µm	50 µm
S9	49 µm	48 µm	49 µm
S10	46 µm	45 µm	46 µm
S11	35 µm	37 µm	36 µm
MD4 (ac)	24 µm	26 µm	broken
MD5 (ac)	28 µm	broken	broken
MD6 (ac)	32 µm	40 µm	broken
MD7 (ac)	37 µm	broken	32 µm
MD8 (ac)	41 µm	broken	34 µm
LV5 (tu)	18 µm	broken	broken
LV6 (ac)	23 µm	broken	broken
LV7 (ac)	26 µm	broken	broken
LV8 (ac)	27 µm	broken	29 µm
LV9 (ac)	28 µm	broken	30 µm
LTS	48 µm	53 µm	46 µm
LTS/TL	14.1%	14.8%	N/A
LTAS (f)	33 µm	broken	32 µm

Notes on diagnostic features. *Echinoderes obtuspinosus* **sp. nov.** can be distinguished from most other congeners by its characteristically short, but very stout lateral terminal spines. Other species with such spines include only *E. abbreviatus* Higgins, 1983, *E. brevicaudatus*, *E. cavernus* and *E. ulsanensis* Adrianov, 1999 in Adrianov & Malakhov, 1999. Especially the latter is relevant in regard to *E. obtuspinosus* **sp. nov.**, because it is described from the Korean southeast coast (see Adrianov & Malakhov 1999), and the two species may very well have overlapping distributions. They also resemble each other in many ways, but can be distinguished by the lateroventral spines on segment 9 that are present in *E. obtuspinosus* **sp. nov.** but lack in *E. ulsanensis*. The new species is much more easily distinguished from *E. abbreviatus* that has only three middorsal spines (see Higgins 1983) opposed to five in *E. obtuspinosus* **sp. nov.**

The two remaining species, *E. cavernus* and *E. brevicaudatus*, both have conspicuously short middorsal spines that never project beyond the posterior segment margin. *Echinoderes brevicaudatus* furthermore has a characteristically strong pectinate fringe on the ventral side of segment 1, and a rather dense covering of cuticular hairs. Besides its distinct difference in length of middorsal spines, *E. cavernus* can be distinguished from *E. obtuspinosus* **sp. nov.** by the presence of relatively long midlateral tubules on segment 10 (mistakenly referred to as “genital setae” by Sørensen *et al.* 2000) and by a different distribution of glandular cell outlets type 2 (gco2). In *E. cavernus* gco2 are present in sublateral positions on segment 2, subdorsal positions on segments 4 to 6, and in midlateral position on segment 9 (referred to as “muscle scars”, “cuticular scars” and “mucous glands” by Sørensen *et al.* 2000).

TABLE 8. Summary of nature and location of sensory spots, glandular cell outlets and spines arranged by series in *Echinoderes obtuspinosus* **sp. nov.** Abbreviations: LA: Lateral accessory; LD: laterodorsal; LV: lateroventral; MD: middorsal; PD: paradorsal; PV: paraventral; SD: subdorsal; SL: sublateral; VL: ventrolateral; VM: ventromedial; ac: acicular spine; (f): female condition of sexual dimorphic character; gco1/2: glandular cell outlet type 1/2; ltas: lateral terminal accessory spine; lts: lateral terminal spine; si: sieve plate; ss: sensory spot; tu: tubule.

Position Segment	MD	PD	SD	LD	SL	LA	LV	VL	VM	PV
1										
2			gco2	gco2	gco2			gco2		
3			ss							
4	ac		gco2						gco1	
5	ac		ss				tu		gco1	
6	ac	ss	ss				ac		gco1	
7	ac	ss	ss				ac		gco1	
8	ac	ss	ss		gco2		ac			gco1
9			ss			si	ac	ss		gco1
10	gco1 gco1		ss					ss		gco1
11						ltas(f?)	lts			

Echinoderes tchefouensis Lou, 1934

(Figures 13–15, Tables 9–10)

Emended diagnosis. Specimens with middorsal spines on segments 4–8; lateroventral tubules on segment 5; lateral accessory spines on segment 8; lateroventral spines on segment 9; laterodorsal tubules on segment 10, being minute in females and of regular size in males. Glandular cell outlets type 2 subdorsal and lateroventral on segment 2 and laterodorsal on segment 8; glandular cell outlets on segment 2 of regular size, outlets on segment 8 extraordinary large.

Type material. Neotype adult male, collected at 28 September 2006, at 79 m depth, from Station MAP-05 (see Table 1) in the East China Sea, 30°31'66"N 125°55'86"E, 400 km south of the Korean Peninsula and east of China (Fig. 1D), mounted in Fluoromount G and deposited at the NHMD under accession number ZMUC KIN-468.

Additional specimens. Mounted in Fluoromount G for LM were found on stations MAP-05 to MAP-08, MAP-15, MAP-23 and MAP-25 to MAP-27, and deposited at NHMD under accession numbers ZMUC KIN-469 to KIN-486 and KIN-554 to KIN-566, and in the personal collections of the authors. Specimens mounted for SEM were found on stations MAP-02, MAP-05 to MAP-09, MAP-15 to MAP-16, MAP-23, MAP-27 to MAP-29 and MAP-31 to MAP-34. All specimens for SEM are kept in the personal collection of MVS. See Fig. 1D for distribution and Table 1 for further details about the stations.

Distribution. *Echinoderes tchefouensis* occurred in several samples (see Table 1 and Fig. 1D), and appears to be rather common in the Korea Strait and the East China Sea. However, it is noteworthy that the species also occurred in samples taken far away from the main study area, inclusive samples from the Malaysian part of Borneo, the Philippines and from Saipan in the Northern Marianas. At the latter locality, *E. tchefouensis* co-occurs with *Triodontoderes anulap* Sørensen & Rho, 2009 that otherwise is known from Micronesia only (see Sørensen & Rho, 2009)

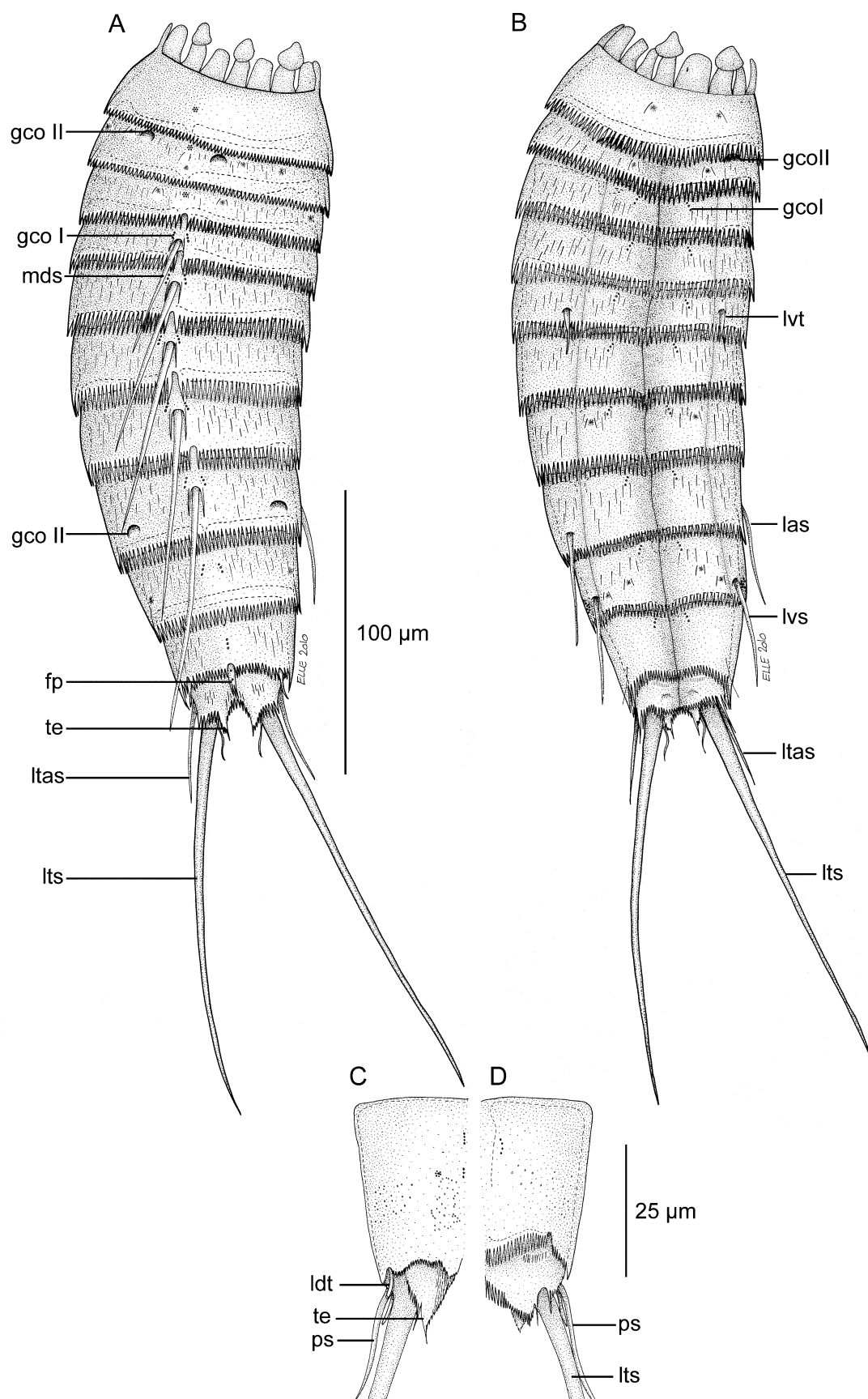


FIGURE 13. Line art illustrations showing general habitus and sexual dimorphism in *Echinoderes tchefouensis* Lou, 1934. A, female, dorsal view; B, female, ventral view; C, segments 10 and 11 in male, dorsal view; D, segments 10 and 11 in male, ventral view. Abbreviations: fp, fringed protuberance; gco I/II, glandular cell outlet type 1/2; las, lateral accessory spine; ldt, laterodorsal tubule; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; lvt, lateroventral tubule; mds, middorsal spine; ps, penile spines; te, tergal extension.

Description. Adult specimens consist of a head, a neck and eleven trunk segments (Figs 13A–B, 15A). Measurements and dimensions are given in Table 9. A summary of sensory spot, spine, tubule and glandular cell outlet positions is provided in Table 10.

The head consists of an introvert and a mouth cone with 9 outer oral styles, composed of two subunits (Fig. 15C). Style bases form a basal plate with folded lateral margins that extend into a pair of anterolateral spikes. The median, external fringe of the style base consists of only two fringe tips, each with bipartite endings (Fig. 15C).

Introvert with 10 spinoscalids in Ring 01, followed by 10, 20 and 10 scalids, respectively, in Rings 02 to 04. Ring 05 with 10 scalids, arranged as two scalids in each uneven numbered section; and Ring 06 with 15 scalids, arranged as one scalid in each uneven numbered section and two scalids in each even numbered one. Hence, described section-wise, uneven numbered sections have 7 scalids, whereas even numbered ones have 6 (Fig. 15B, see also Fig. 8 for an overview of scalid distribution in a species with a corresponding pattern). Additional leaf-like scalids, not following a pentaradial pattern, are present in ring 07. These leaf-like scalids are present as one scalid in sections 1, 5, 6 and 7, and two scalids in sections 3 and 9.

The neck consists of 16 placids, all measuring 9 μm in length and 7 μm in width at bases, except midventral placid that measures 10 μm in width. Placids number 2 and 16 (counting clockwise from midventral placid) with broad trichoscalid plate and attached trichoscalid (Fig. 14B). Smaller trichoscalid plates with trichoscalids on placids number 6, 8, 10, and 12 (Fig. 14A).

Segment 1 consists of one complete cuticular ring (Figs 13A–B, 14A–B). Type 1 glandular cell outlets present in middorsal position (Figs 13A, 14A). One pair of minute sensory spots present in ventrolateral position (Figs 13B, 14B, 15F); each sensory spot has a single, associated cuticular hair (Fig. 15F). Cuticular hairs are otherwise either missing completely or only present sporadically on the dorsal side. Posterior margin with pectinate fringe; fringe tips on dorsal and lateral sides appear short and broad whereas the ventral ones are narrower, but longer and conspicuously stronger.

Segment 2 consists of one complete cuticular ring. Sensory spots are present in middorsal, subdorsal, laterodorsal (Figs 14A, 15E) and ventromedial positions; sensory spots on tergal plate with two associated cuticular hairs located anterior to the sensory spots (Figs 13B, 15E). Glandular cell outlets of type 2 located in subdorsal and lateroventral positions (Figs 13A–B, 14A–B, 15E–F); lateroventral pair is often partly or completely covered by the strong pectinate fringe from the preceding segment. Type 1 glandular cell outlet present in middorsal position, near anterior margin of segment. Cuticular hairs are few and follow almost a straight, transverse line on the dorsal and lateral sides; a few more and longer hairs present on the ventral side. Pectinate fringe as on preceding segment.

Segment 3 and following eight segments consist of one tergal and two sternal plates (Fig. 13B). Type 1 glandular cell outlet present in middorsal and ventromedial positions. Paired sensory spots, each with two associated cuticular hairs, located in subdorsal and midlateral positions. Other cuticular hairs are bracteate, scattered on anterior half of the tergal plate and in two large ventrolateral patches on the sternal plates; paraventral positions without hairs and filiform extensions. Well-developed pectinate fringe present along posterior segment margin; posterior margin with middorsal incision in which the middorsal spine of the following segment fits during strong contraction of the trunk segments (Fig. 13A).

Segment 4 with long middorsal spine and paired type 1 glandular cell outlets present in paradorsal and ventromedial positions (Figs 13A); glandular cell outlets cannot be visualized with SEM, but with LM they appear as three dots on a row (see Fig. 14C for similar structures on following segments). Posterior segment margin with middorsal incision. Cuticular hairs and pectinate fringe as on preceding segment.

Segment 5 with long middorsal spine and pair of lateroventral tubules (Figs 13A–B, 14C). Type 1 glandular cell outlets present in paradorsal (Fig. 14C) and ventromedial positions. Posterior segment margin with middorsal incision. Cuticular hairs and pectinate fringe as on preceding segment.

Segments 6 and 7 with long middorsal spines (Figs 13A–B, 14C). Type 1 glandular cell outlets present in paradorsal (Fig. 14C) and ventromedial positions (Fig. 13B). Segment 7 furthermore with a pair of ventrolateral sensory spots. Posterior segment margin with middorsal incision. Cuticular hairs and pectinate fringe as on segment 5.

Segment 8 with long middorsal spine and pair of lateral accessory spines (Figs 13B, 14E). Type 1 glandular cell outlets present in paradorsal and ventromedial positions (Fig. 14C). A pair of very large and conspicuous type 2 glandular cell outlets present in laterodorsal positions (Figs 13A, 14C–D, 15A, D). Posterior segment margin without middorsal incision. Cuticular hairs and pectinate fringe as on preceding segments.

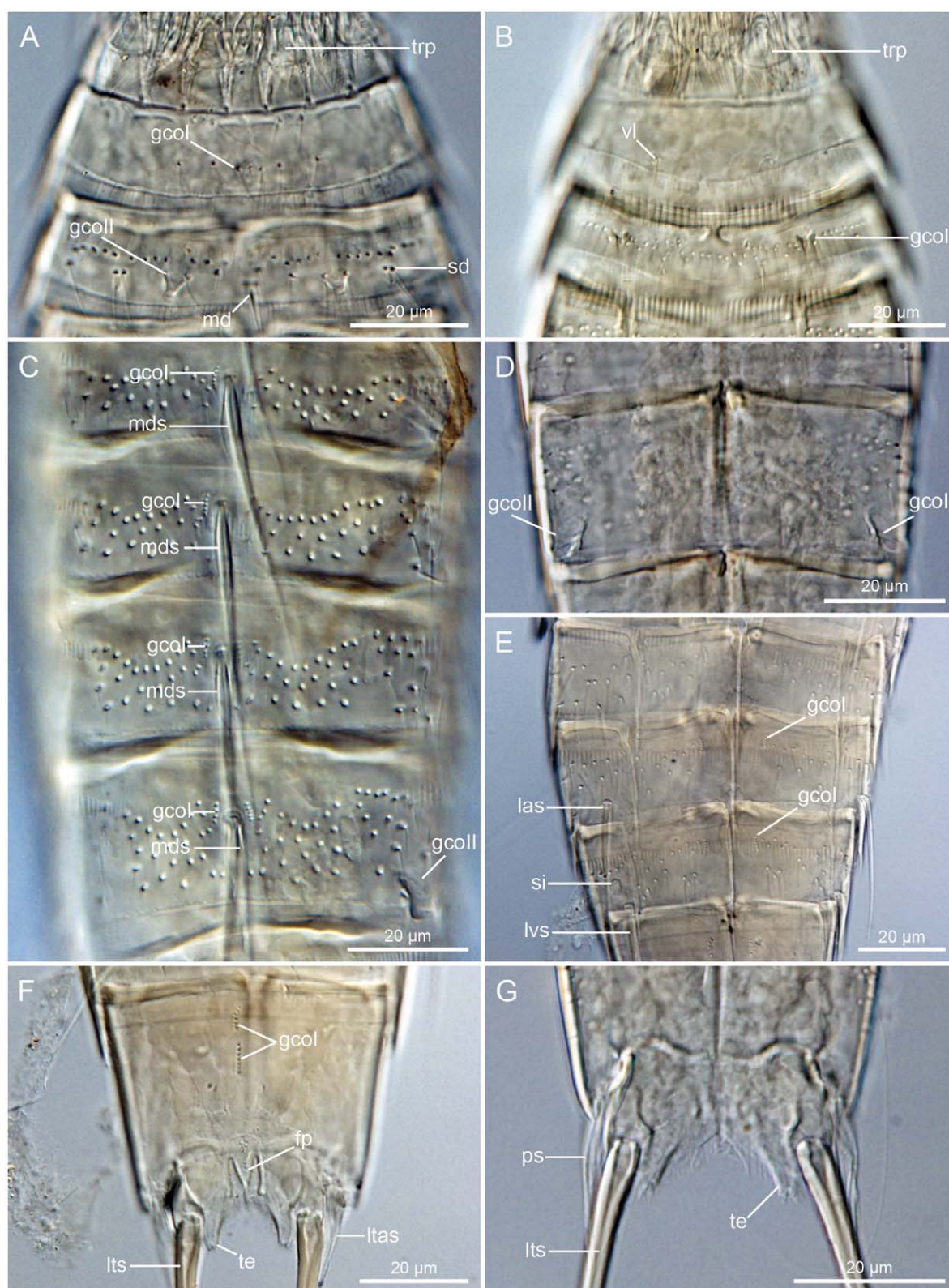


FIGURE 14. Light micrographs showing details in neck and trunk morphology of *Echinoderes tchefouensis* Lou, 1934, displaying male neotype, ZMUC KIN-468 (A–B, D, G), and two other female non-types, ZMUC KIN-469 (C), ZMUC KIN-474 (E–F): A, neck and segments 1 to 2, dorsal view; B, neck and segments 1 to 2, ventral view; C, segments 5 to 8, dorsal view; D, segment 8, focused on laterodorsal gco2; E, segments 7 to 9, ventral view; F, segments 10 to 11 in female, dorsal view; F, segments 10 to 11 spines in male, ventral view. Abbreviations: fp, fringed protuberance; gco I/II, glandular cell outlet type 1/2; las, lateral accessory spine; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; md, middorsal sensory spot; mds, middorsal spine; ps, penile spines; sd, subdorsal sensory spot; si, sieve plate; te, tergal extension; trp, trichoscalid plate; vl, ventrolateral sensory spot.

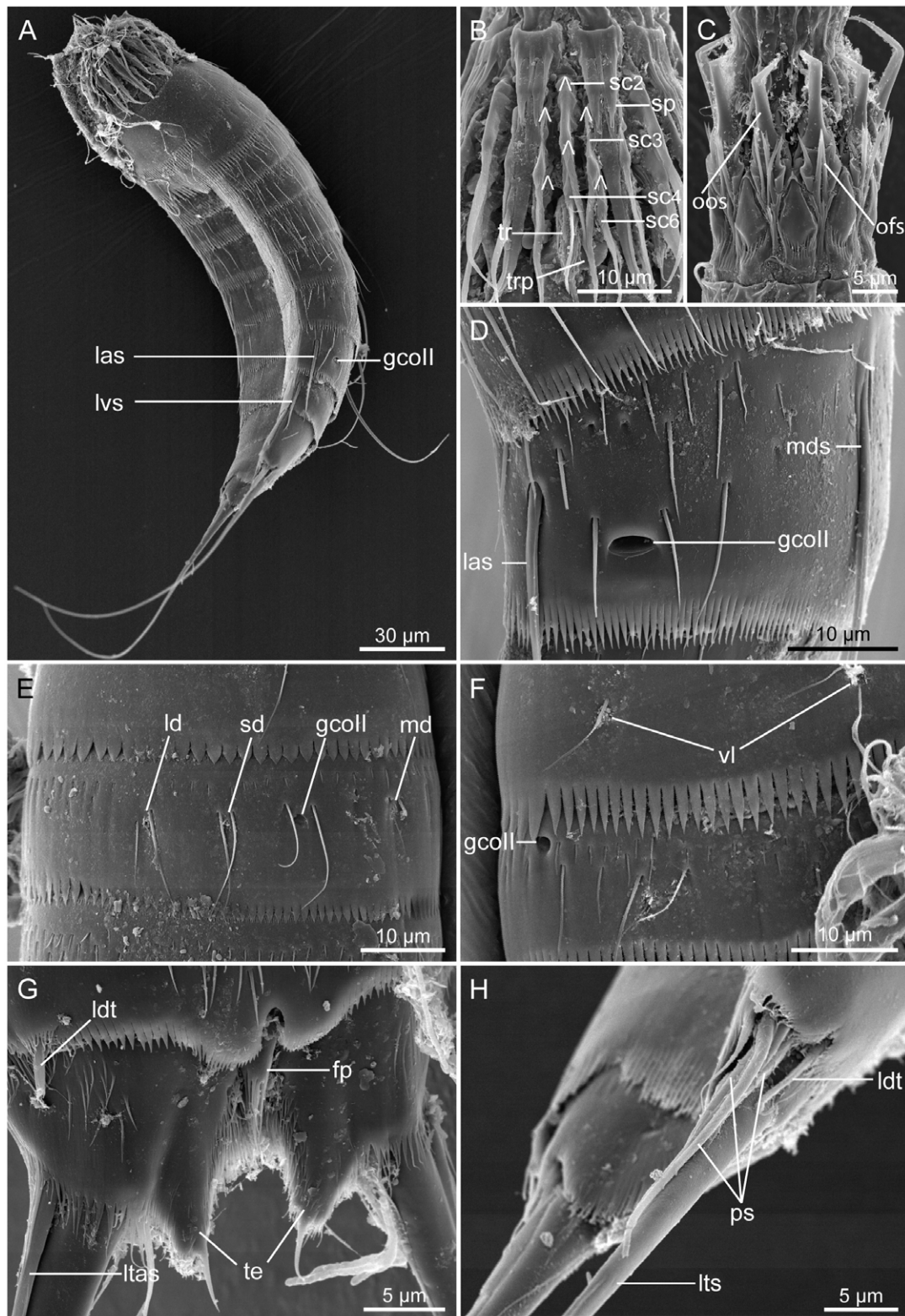


FIGURE 15. Scanning electron micrographs showing overview and details in head and trunk morphology of *Echinoderes tchefouensis* Lou, 1934: A, ventrolateral overview of whole specimen; B, detail of head, showing introvert section 4; C, detail of head showing mouth cone; D, segment 8, lateral view; E, segment 2, dorsolateral view; F, segments 1 and 2, ventral view; G, segment 11 in female, dorsal view; H, segments 11 in male, lateral view. Abbreviations: fp, fringed protuberance; gco II, glandular cell outlet type 2; las, lateral accessory spine; ld, laterodorsal sensory spot; ldt, laterodorsal tubule; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; md, middorsal sensory spot; mds, middorsal spine; ofs, outer fringe of style basis; oos, outer oral styles; ps, penile spines; sc, scalids; sd, subdorsal sensory spot; sp, spinoscalids; te, tergal extension; tr, trichoscalid; trp, trichoscalid plate; vl, ventrolateral sensory spot. Digits after the labels refer to the introvert ring numbers. Lambda symbols Λ mark attachment point of scalids.

Segment 9 without middorsal spine, but with spines in the lateroventral position (Fig. 13B, 14E). Type 1 glandular cell outlets present in paradorsal ventromedial positions. Pairs of laterodorsal, ventrolateral and ventromedial sensory spots present. Small, rounded sieve plates present in the lateral accessory position (Fig. 14E). Cuticular hairs and pectinate fringe as on preceding segments.

Segment 10 without acicular spines, but with a pair of short, laterodorsal tubules that emerge from a position under the posterior segment margin (Figs 13C, 15G–H); the tubules could not be clearly visualized with LM, but from SEM observations the lengths are estimated to ca. 4–8 μm . Two type 1 glandular cell outlets are present in a middorsal position (Fig. 14F); one additional pair present in ventromedial positions. Tergal plate with few or no cuticular hairs; sternal plates with bracteate hairs on anterior half of segment. Pectinate fringe weak to moderate on tergal plate, but with long and strongly developed fringe tips on sternal plates (Fig. 15G–H). A broad protuberance with fringed end is present middorsally at the intersection between segment 10 and 11 (Figs 13A, 14F, 15G). The protuberance appears to be restricted to females only, but this is difficult to determine since it in strongly contracted specimens often is covered by segment 10.

Segment 11 with lateral terminal spines (Figs 13A–B, 14F–G). Females furthermore with pair of rather short and somewhat flexible lateral terminal accessory spines, equipped with a row of minute hooks on their external lateral sides. Males with three pairs of penile spines that emerge from the intersegmental joint with the previous segment (Figs 13C–D, 14G, 15H); two penile spines are quite short, whereas the third one is long and flexible. Two type 1 glandular cell outlets are present in a middorsal position, underneath the fringed protuberance. Cuticular hairs are present in two laterodorsal clusters only (Fig. 15G). Tergal plate terminates into rather short, obliquely truncate extensions equipped with a spinose tip (Figs 13A–C, 14F–G, 15G); margin of sternal plates almost straight, with pectinate fringe, but no particular extensions (Fig. 13B–D).

Comparison with original description. *Echinoderes tchefouensis* was originally described from the Yantai area on the Chinese Northeast Coast, about 320 km west of the Korean Peninsula (see Lou 1934). The original description by Lou, 1934 is generally rather poor, and it basically only describes *E. tchefouensis* as a species with middorsal spines on segments 4 to 8, and lateral spines on some segments that are not specified any further. From this information alone, it would not be possible to identify the species, and it would probably be most correct to consider it a *nomen nudum*. However, during his numerous collectings in East Asia, Robert P. Higgins sampled specimens of *Echinoderes* from the coast of Yantai and he considered these to be conspecific with *E. tchefouensis*. The specimens were never used for an actual redescription of the species, but their existence and putative identity with *E. tchefouensis* is mentioned by Higgins and Kristensen (1988) under the description of *Echinoderes eximus* Higgins & Kristensen, 1988, and it is noted that they have a characteristic spine distribution in the lateral series, with lateral spines on segments 5, 8 and 9 only. Subsequently, it has been broadly accepted that *E. tchefouensis* is characterized by the presence of middorsal spines on segments 4 to 8, and lateral spines on segments 5, 8 and 9, and the species has been referred under this diagnosis in several studies and keys (e.g. Adrianov and Malakhov 1999; Adrianov et al. 2002a). Since the specimens used in the present study fit this diagnosis, and some of them are collected only 500 km from the Chinese type locality, we consider these specimens conspecific with *E. tchefouensis* Lou (1934) *sensu* Higgins.

It would surely have been preferable to have specimens from the exact type locality, but the wide distribution of the specimens collected for present study indicate that the species is very common in the entire region. From this study alone, the species appears to have a distribution that stretches from Malaysia in the south and the Saipan Islands in the West Pacific, to the Korean Peninsula in the north.

Notes on diagnostic features. *Echinoderes tchefouensis* is easily recognized by its almost unique spine pattern in the lateral series. The combination of having only lateroventral tubules on segment 5, lateral accessory spines on segment 8 and lateroventral spines on segment 9 is solely shared with *E. eximus* that is known from Greenland only (see Higgins & Kristensen 1988). These two species, however, show great resemblance. Besides having identical spine patterns in the dorsal and lateral series, *E. eximus* also has subdorsal and lateroventral glandular cell outlets type 2 (gco2) on segment 2. These outlets were reported as “cuticular scars” by Higgins & Kristensen (1988), but are obviously gco2. This was confirmed by re-examinations of two paratypes (ZMUC KIN-27 and 28) that are deposited at the NHMD. Examination of these paratypes furthermore revealed the presence of laterodorsal gco2 on segment 8 as well. These structures are not mentioned by Higgins & Kristensen (1988) and they are positioned so close to the lateral edge of the specimens that it is difficult to get a good view of them. Besides the ‘cuticular scars’ (=gco2) on segment 2, Higgins & Kristensen (1988) reports the presence of two pairs of ‘prominent truncate

muscle scars' on the tergal plate of segment 10. The structures are documented on Figures 48 in Higgins & Kristensen (1988) and are most likely gco2 as well. Such openings are not present on segment 10 in *E. tchefouensis*.

TABLE 9. Measurements of adult *Echinoderes tchefouensis* Lou, 1934 from the Korea Strait and East China Sea (Stations: MAP-05, 6, 7, 23), including number of measured specimens (n) and standard deviation (S.D.). Abbreviations: (ac): acicular spine; (f): female condition of sexual dimorphic character; LAS: lateral accessory; LD: laterodorsal; LTAS: lateral terminal accessory spine; LTS: lateral terminal spine; LV: lateroventral; MD: middorsal; MSW-5: Maximum sternal width, measured on segment 5 in this species; S: segment lengths; SW-10, standard width, always measured on segment 10; TL: trunk length; (tu): tubule; VL: ventrolateral. Dash – indicates that the structure could not be measured.

Character	n	Range	Mean	S.D.
TL	10	225 – 254 µm	245 µm	10.85 µm
MSW-5	10	43 – 49 µm	46 µm	2.15 µm
MSW-5/TL	10	17.0 – 21.3%	18.9%	1.41%
SW-10	10	39 – 4 µm	42 µm	1.78 µm
SW-10/TL	10	15.7 – 19.1%	17.0%	1.24%
S1	10	23 – 26 µm	25 µm	0.99 µm
S2	10	24 – 27 µm	26 µm	1.06 µm
S3	10	26 – 29 µm	27 µm	0.95 µm
S4	10	27 – 31 µm	28 µm	1.34 µm
S5	10	28 – 34 µm	30 µm	1.93 µm
S6	10	30 – 34 µm	32 µm	1.14 µm
S7	10	32 – 36 µm	34 µm	1.60 µm
S8	10	34 – 39 µm	36 µm	1.55 µm
S9	10	32 – 37 µm	35 µm	1.35 µm
S10	10	34 – 43 µm	38 µm	2.90 µm
S11	10	21 – 25 µm	23 µm	1.66 µm
MD 4 (ac)	7	44 – 54 µm	47 µm	3.50 µm
MD 5 (ac)	7	49 – 67 µm	59 µm	6.54 µm
MD 6 (ac)	7	51 – 73 µm	63 µm	1.41 µm
MD 7 (ac)	5	73 – 78 µm	75 µm	8.96 µm
MD 8 (ac)	7	77 – 89 µm	82 µm	2.17 µm
LV 5 (tu)	4	12 – 17 µm	14 µm	2.22 µm
LAS 8 (ac)	8	22 – 35 µm	30 µm	4.98 µm
LV9 (ac)	5	23 – 28 µm	26 µm	2.28 µm
LD 10 (tu)	–	–	–	–
LTS	9	138 – 198 µm	165 µm	25.93 µm
LTS/TL	9	54.5 – 79.8%	66.8%	10.15 %
LTAS (f)	3	21 – 23 µm	22 µm	1.00 µm

Besides, the spine formulas and distribution of gco2 on segments 2 and 8, another intriguing similarity between the two species regards the tube-like and terminally fringed protuberance found middorsally in *E. tchefouensis* at the intersection between segments 10 and 11. A very similar structure appears to be present in *E. eximus* also, hence this could be one additional character shared by the two species. To our knowledge, such a structure has not previously been reported for any other kinorhynch. However, examinations of the holotype of *E. maxwelli* Omer-Cooper 1957 revealed that a somewhat similar structure may be present in this species as well. In general, *E. tchefouensis* and *E. eximus* share several similarities, and it may be difficult to distinguish between the two species. The most characteristic differences are probably the putative type 2 glandular cell outlets on the tergal plate of segment 10, present in *E. eximus* (see Higgins & Kristensen 1988) but absent in *E. tchefouensis*, the somewhat different shapes of the tergal extensions of the two species, and the presence of short laterodorsal tubules on segment 10 in *E. tchefouensis*.

Another species that also attracts some interest in relation to *E. tchefouensis* is *Echinoderes caribiensis* Kirsteuer, 1964. In its lateral series, the species has spines on segments 5, 8 and 9, which is the same overall configuration as found in *E. tchefouensis* and *E. eximus*. Kirsteuer (1964) does not indicate clearly if the spines on segment 8 are shifted to a lateral accessory position, but knowing the lateral spine formulas in the two latter species, one may speculate if the same pattern is expressed in *E. caribiensis*. Besides this potential similarity, *E. caribiensis* is easily distinguished from *E. tchefouensis* and *E. eximus*. It has no middorsal spines, and the lateral terminal spines are rather short. Information on gco2 or similar structures is not available.

TABLE 10. Summary of nature and location of sensory spots, glandular cell outlets and spines arranged by series in *Echinoderes tchefouensis* Lou, 1934. Abbreviations: LA: Lateral accessory; LD: laterodorsal; LV: lateroventral; MD: middorsal; ML: midlateral; PD: paradorsal; SD: subdorsal; VL: ventrolateral; VM: ventromedial; ac, acicular spine; (f), female condition of sexual dimorphic character; gco1/2, modified glandular cell outlet type 1/2; gfs, gland with funnel-shaped subcuticular structure; ltas, lateral terminal accessory spine; lts, lateral terminal spine; si, sieve plate; ss, sensory spot; tu, tubule.

Position Segment	MD	PD	SD	LD	ML	LA	LV	VL	VM
1	gco1							ss	
2	gco1,ss		ss,gco2	ss			gco2		ss
3	gco1		ss		ss				gco1
4	ac	gco1							gco1
5	ac	gco1					tu		gco1
6	ac	gco1							gco1
7	ac	gco1						ss	gco1
8	ac	gco1		gco2		ac			gco1
9		gco1		ss		si	ac	ss	gco1,ss
10	gco1,gco1			tu					gco1
11	gco1,gco1					ltas (f)	lts		

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